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Zooming out the microscope on cumulative cultural evolution: ‘Trajectory B’ from animal to human culture

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It is widely believed that human culture originated in the appearance of Oldowan stone-tool production (circa 2.9 Mya) and a primitive but effective ability to copy detailed know-how. Cumulative cultural evolution is then believed to have led to modern humans and human culture via self-reinforcing gene-culture co-evolution. This outline evolutionary trajectory has come to be seen as all but self-evident, but dilemmas have appeared as it has been explored in increasing detail. Can we attribute even a minimally effective know-how copying capability to Oldowan hominins? Do Oldowan tools really demand know-how copying? Is there any other evidence that know-how copying was present? We here argue that this account, which we refer to as “Trajectory A”, may be a red herring, and formulate an alternative “Trajectory B” that resolves these dilemmas. Trajectory B invokes an overlooked group-level channel of cultural inheritance (the Social Protocell) whereby *networks* of cultural traits can be faithfully inherited and potentially undergo cumulative evolution, also when the underpinning cultural traits are apelike in not being transmitted via know-how copying (Latent Solutions). Since most preconditions of Trajectory B are present in modern-day *Pan*, Trajectory B may even have its roots considerably *before* Oldowan toolmaking. The cumulative build-up of networks of non-cumulative cultural traits is then argued to have produced conditions that both called for and afforded a gradual appearance of the ability to copy know-how, but considerably later than the Oldowan.

Introduction

“What are the roots of human culture?” was listed as one of the 125 Big Questions of our time in the 125th anniversary issue of *Science* (“What we don’t know,” 2005). Since then, substantial progress has been made in answering and, perhaps in particular, resolving it into networks of more focused (“smaller”) and empirically more accessible questions. This has happened amid a widening and deepening involvement of a variety of academic fields, such as genetics, archaeology, primatology, cognitive science, and palaeontology,

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along with technological and methodological innovation within these fields, including not least new laboratory techniques.

As we have hereby "zoomed in" on this Big Question, the concept of "cumulative cultural evolution" has emerged as a key part of its answer (Boyd and Richerson, 1995; Dean et al., 2012; Henrich, 2016; Tennie et al., 2020; Tomasello, 1999). As opposed to "animal culture", human culture retains and refines complex "know-how"[1] (in behaviours, artefacts, institutions, etc.) even beyond individual limits to comprehension and creativity, and humans cannot survive unless enculturated into systems of such knowledge. But understanding the significance of this explosive human variety of cumulative culture (henceforth denoted "cumulativity" unless otherwise specified) is easier than understanding what it is, how it works, how it arose, and (given how widespread animal culture is, see e.g., Allen, 2019; Galef and Laland, 2005; Schuppli and Schaik, 2019) why it came to dominate only in the genus *Homo*.[2]

Zooming in further to understand cumulativity, *copying* in cultural transmission has come to the fore as the core issue. For cumulative cultural evolution (as defined above) to be possible, variants of cultural traits must be transmitted without too much distortion. If not, variants of the past will be lost, and cultural evolution cannot build upon them, which precludes the evolution of cultural traits beyond the limits of what individuals may invent themselves (please see Appendix A for a word list).

However, also copying can be further resolved. As we have zoomed in even more to discern *how* cultural knowledge gets transmitted, copying has emerged as a delicate task that calls for specialised abilities. Cultural transmission therefore *combines* key elements of copying with individual invention. Apes will for example copy key aspects of cultural traits (including the know-*what*, know-*where*, and so on, which tend to be observationally transparent enough for them to copy) to focus their substantial inventive abilities on the task of *re-inventing* the crucial *know-how* aspects, which in general are observationally opaquer and much harder to copy (see Fig. 1).[3] Since know-how that is re-invented by similar agents, with similar motives, and in similar contexts, tends to also turn out highly similar know-how (e.g., Borg et al., 2023), cultural transmission in apes is easily mistaken for a low-fidelity type of know-how copying.

To summarise a long and still-evolving story, we hereby identify *the origin and evolution of know-how copying* as the crux of the modern scientific enquiry into the roots of human culture. We may now summarise the arguably main structuring position of current thinking: *Homo* has gained an increasingly sophisticated and general capacity for transmitting cultural traits via know-how copying. Other primates, including ancestral hominins, lacked this capacity (or it was insufficient), and while they would copy the know-what, know-where, and so on, of cultural traits, they had to creatively re-invent the know-how each cycle. *With* know-how copying, cumulative cultural evolution can take off since the details of know-how can persist. *Without* know-how copying, cumulative culture will not take off since the details of know-how cannot persist. The only imaginable conclusion seems to be that *the roots of human culture must lie in the emergence and honing of special abilities for know-how copying in cultural transmission.*

When we let this theoretical understanding structure our understanding of human pre-history, a macroevolutionary picture flows from a beginning that can be outlined as follows: The appearance of a know-how copying ability that adequately supported cumulative know-how was heralded by Oldowan sharp stone-tool production 2.9 Mya in East Africa (see Potts et al., 2023; until recently at 2.6 Mya; see Patterson et al., 2019; Semaw et al., 2003), in the context of early *Homo* and an incipient large game carnivory niche that began with scavenging. We refer to this widely held view as "Trajectory A."

Trajectory A, however, has reached what we argue is an impasse. Zooming in on its details has revealed that know-how copying is harder to attribute to early *Homo* than widely believed and that it may not even be needed for explaining Oldowan toolmaking. This undermines Trajectory A and threatens to rob it of much of its explanatory power, since if cumulative know-how arose much later than the Oldowan, the origin of humanlikeness in culture would seem to end up well into the evolution of *Homo*—possibly after *Homo* began actively hunting, after the evolution of its conspicuously large brain and overall humanlike physiology, and after it spread across the Old World into more and more varied types of environments. In other words, *after* a range of events that most tend to attribute to cumulative culture.

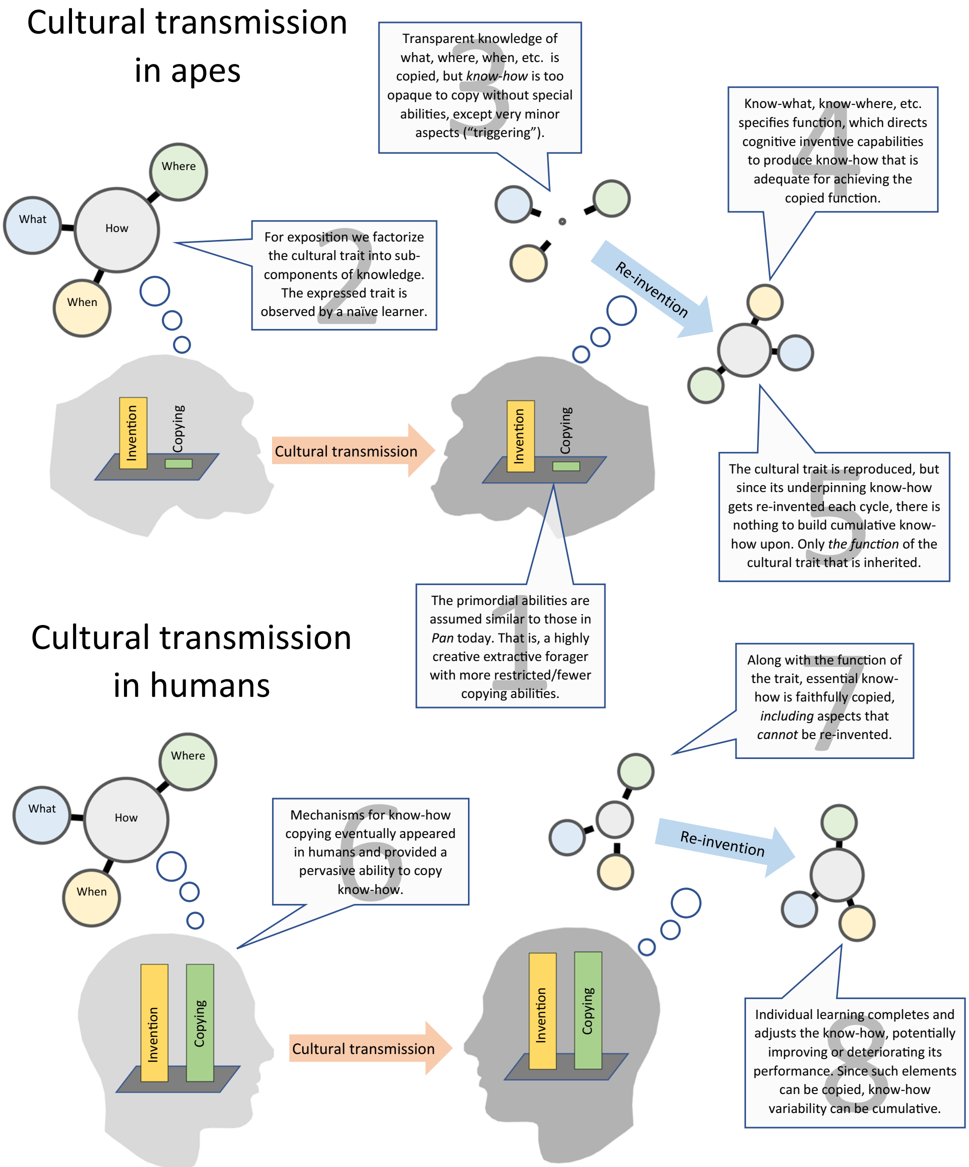
But if the roots of human culture do *not* lie in know-how copying, where could they plausibly lie? We here outline an alternative "Trajectory B" that comes into view only if we reverse the current trend and zoom *out* again—though guided by what we have learned by zooming in. The key feature of Trajectory B is that cultural inheritance and cumulative cultural evolution here first arises *at the cultural group level* and on the basis of *networks* of non-cumulative cultural traits. Trajectory B requires no attribution of humanlike adaptations to apelike ancestral apes, and apart from a key ecological factor, we argue that the necessary mechanisms were likely present already in the last common ancestor between *Homo* and *Pan* (and that they *remain* present in *Pan* today). A *different* kind of cumulative culture could hereby have originated *even earlier* than with the Oldowan toolmakers.

Trajectory B combines two different models. *The Social Protocell Hypothesis* (SPH; see Andersson and Czárán, 2023; Andersson and Törnberg, 2019; Davison et al., 2021) proposes that a mechanism for cultural reproduction, inheritance and individuation may arise spontaneously on the level of social communities, via a fortuitous confluence of separately explainable factors, most importantly ape culture and a particular type of social group dynamics that is shared between hominins and panines. We then use *the Zone of Latent Solutions* (ZLS; see Tennie et al., 2009; Tennie et al., 2020) to understand and explore the limits of cultural organisation before the appearance of know-how copying.

We begin by arguing that know-how copying has turned out to be *less needed, less likely, and less supported* by empirical evidence than most suppose as an explanation of hominin culture until well after the Oldowan, and that this undermines Trajectory A. Trajectory B is then introduced as an alternative that avoids these problems. To do this we first discuss cultural organisation under Trajectory B. Guided by the *Zone of Latent Solutions*, we introduce and specify units and interactions, across levels of organisation and selection, to describe how simple networks of cultural traits could arise even in ape culture today. We then move to the mechanisms of cumulative culture under Trajectory B, describing how the *Social Protocell* could cause networks of cultural traits to evolve into group-level units of selection in their own right. Trajectory B is then contextualised empirically via three preliminary accounts of (i) the roots of human culture, (ii) how its group-level cumulativity would boost itself, (iii) and how it accounts also for the eventual appearance of know-how copying. Finally, we summarise the proposition and discuss to which extent Trajectory B can be argued to be *more needed, likely, and supported* than Trajectory A.

Trajectory A at an impasse

The impasse we claimed has appeared along Trajectory A may be summarised by stating that know-how copying is *less likely* and *less needed* and *less supported* for explaining the culture of the Oldowan toolmakers than widely assumed. In this section, we



Cultural transmission in apes

Cultural transmission in humans

1 The primordial abilities are assumed similar to those in *Pan* today. That is, a highly creative extractive forager with more restricted/fewer copying abilities.

2 For exposition we factorize the cultural trait into sub-components of knowledge. The expressed trait is observed by a naïve learner.

3 Transparent knowledge of what, where, when, etc. is copied, but *know-how* is too opaque to copy without special abilities, except very minor aspects ("triggering").

4 Know-what, know-where, etc. specifies function, which directs cognitive inventive capabilities to produce know-how that is adequate for achieving the copied function.

5 The cultural trait is reproduced, but since its underpinning know-how gets re-invented each cycle, there is nothing to build cumulative know-how upon. Only *the function* of the cultural trait that is inherited.

6 Mechanisms for know-how copying eventually appeared in humans and provided a pervasive ability to copy know-how.

7 Along with the function of the trait, essential know-how is faithfully copied, *including* aspects that *cannot* be re-invented.

8 Individual learning completes and adjusts the know-how, potentially improving or deteriorating its performance. Since such elements can be copied, know-how variability can be cumulative.

Fig. 1 Cultural transmission in apes and humans. *Apes* copy the function of cultural traits (mainly via transparent aspect like know-what, know-where, know-why, etc.) to focus their inventive capacity to supply the copied function with adequate know-how. This functionally reproduces the cultural trait in the learner, but know-how is not inherited (except possibly fragments via "triggering", e.g., how sneezes and laughs spread) and cannot be cumulative. *Humans* can copy know-how and judge which details to focus on, and since details of know-how can make it across, they can also be preserved and cumulatively built upon over time, beyond what the learner would have been able to re-invent had it not copied.

review these dilemmas to set the scene for Trajectory B and motivate why we should look for alternative explanatory routes (we again point to the glossary in Appendix A).

Oldowan know-how copying is *less likely* than widely assumed. The appearance of know-how copying in Oldowan hominins is widely seen as quite likely, and its evolution tends to be imagined somewhat like the straightforward scenario that Fig. 2A abstractly illustrates. The idea is that some simple *pre-adapted* type of know-how copying appeared and gradually improved under selection for the benefits it conveyed by enabling cumulative culture (not least tool technology). We will argue, however, that plausible know-how copying abilities in Oldowan hominins would be too simple to be effective as pre-adaptations for cumulative culture. Gradual improvements in that role would thereby not have been selected for (they would face a start-up problem, see Fig. 2B).

Let us begin by noting that copying is far from universally preferable over inventing the knowledge oneself. The dilemma of choosing between these options is well-researched as a discrete choice between social and individual learning, where the former implies copying and the latter re-invention (see e.g., Enquist et al., 2007; Feldman et al., 1996; Rendell et al., 2010; Rogers, 1988). Which option is preferable has turned out to depend on a variety of factors, and in particular the rate at which the value of copied knowledge deteriorates over time. For example, if the setting of the knowledge changes rapidly, invention will be favoured since it takes current conditions into account, while copied knowledge will rapidly become outdated.

But know-how copying still gets an easier ride than it deserves here. If we use these models to understand *evolutionary* rather

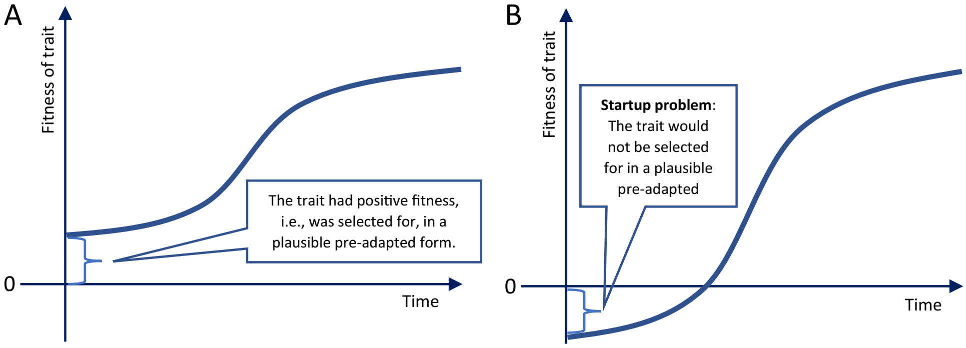


Fig. 2 A start-up problem. We illustrate the fitness of a trait under selection for some adaptive function in two scenarios **A**, **B**. The starting points are *pre-adaptations* that are candidate starting points for evolution under the selection pressure that we consider, but present due to *other* selection pressures. For example, ventral fins evolved for swimming, but were adequately pre-adapted for terrestrial locomotion in some fish. That is, they afforded the evolution of legs under selection for that function. The lefthand case (**A**) is straightforward since the pre-adapted trait has positive fitness and is selected for from the outset under the new selection pressure. In the righthand case (**B**), however, we have a "start-up problem" since the candidate pre-adaptation has negative fitness and will not be selected for under the new selection pressure. For example, if forearms are candidate pre-adaptations for flight in birds, we are in case **B** since forearms would not be selected for at all under selection for flight. The discovery of dinosaur down for isolation, feathers for display, and feathered forearms for gliding, then provides use with the needed bridge to a working pre-adaptation for flight. With gliding as a pre-adaptation, we may be in case **A**.

than individual choices, the fact that they take the *ability* to copy for granted becomes misleading when it comes to know-how. Know-how is inherently complex and opaque since it specifies specific and detail-sensitive ways to wrestle desired outcomes from an environment that, at best, is indifferent to our desires (like raw materials) and, at worst, hostile to them (e.g., defensive adaptations). So even when those models would deem know-how copying to be preferable, an *evolutionary* shift to copying is still far from a simple matter of choice.

It is also well to point out that *any* type of know-how copying will not explain the evolution of human culture. For example, the know-how copying that has been proposed to underpin cumulative cultural bird- and whale songs (see e.g., Fehér et al., 2009; Garland et al., 2022) may be adapted to deal specifically with narrow domains of know-how (to the extent that they turn out to be genuine examples; see Mercado, 2022) with fixed and limited domains of variation. An ability to copy such know-how may thereby avoid the complexity and opaqueness we described above, which would also make it unsuited as an evolutionary starting point for domain-general know-how copying in the future, which is what is relevant to us.

If a general ability to copy know-how nevertheless arises, the next thing we must ask is whether its performance is adequate for supporting cumulative evolution. Transmission fidelity is a crucially important such consideration since unless selection for adaptive know-how variants outpaces the rate at which copying errors are made, *the errors* will cumulate and rapidly corrupt the know-how, regardless of how stable the environment is (Andersson, 2013; Dean et al., 2012; Tomasello et al., 1993). This has been likened with a "treadmill of cultural loss" (see Henrich, 2004b; Kline and Boyd, 2010) where the error rate represents the speed of the treadmill, and the runner's ability to keep pace represents the ability to compensate for errors.

It is widely acknowledged that copying fidelity must reach some substantial level to be sufficient for supporting cumulative culture. Human cultural copying is for this reason often qualified as "high-fidelity copying" in the literature, to differentiate it from inadequate apelike "low-fidelity copying". As we have argued, however, apelike cultural transmission involves at most marginal copying of know-how (e.g., if we qualify "triggering" as copying; see Sperber, 2000). Its semblance of know-how copying is superficial and due to that similar agents solving similar problems in similar settings tend to invent similar know-how. The difference is thereby better seen as qualitative (copying vs. re-invention) rather than quantitative (low- vs. high-fidelity copying); see also *Introduction* and Tennie, et al. (2020), and the suggestion is that unless one can copy with sufficient fidelity, it is best not to copy at all.

This intuition is confirmed, and may be extended, via fundamental theoretical research that shows how gradual changes in copying fidelity produce *abrupt* changes in evolutionary cumulativity. The reason is that the interplay between selection and error rate produces a non-linear dynamical phenomenon known as an *error catastrophe* that imposes a sharp *error threshold* (e.g., Biebricher and Eigen, 2006; Eigen and Schuster, 1977; Maynard-Smith and Szathmáry, 1995). To illustrate in the cultural domain, say we observe how the evolutionary persistence of some piece of know-how (of some specific complexity) varies as we vary the copying fidelity. At zero fidelity, unsurprisingly, persistence will be zero. What may be more surprising is that as we increase fidelity, persistence *remains* at zero until it suddenly gains *indefinite* persistence at some critical point (see Andersson, 2011, 2013; Andersson and Törnberg, 2016). Essentially, the more complex the know-how, the higher its critical threshold of fidelity will be.

But know-how copying is not "home safe" even with adequate fidelity. More factors must be in place for cumulative evolution to work (see Shea, 2009). One particularly important such factor has to do with the idiosyncrasy that cultural selection happens via learner decisions. Complexity and opaqueness make know-how not only hard to invent and copy, but also hard to properly *assess the adaptive benefits of.* Such assessments, in turn, serve to motivating learners to actually learn and use cultural traits. The adaptive value of an ability to copy know-how would thereby hinge on the presence of *additional* abilities to assess the adaptive value also of complex and opaque cumulative cultural behaviours.

Consider for example a scenario where know-how copying enters gradually as a support for re-invention (as "guided variation", see Boyd and Richerson, 1985, or "cultural attraction", see Sperber, 1996) to selectively copy key details of know-how, such as important actions that are too causally opaque to be re-invented, but transparent enough to be easy to copy (clearly observable). Even if know-how is only used for key details, the learner still has to judge whether details seem pointless because they *are* pointless (or even ruinous for the function) or because they are unusually clever. Humans have some ways of determining this. High-quality role models with comparably fewer pointless or erroneous details in their know-how can be selected via learning- (or model) biases based on easier-to-assess proxies for the adaptivity of knowledge (e.g., skill bias, success bias, prestige bias; see e.g., Boyd and Richerson, 1985; Jiménez and Mesoudi, 2019). However, the underpinning capacities of such biases are highly derived in *Homo*, and any precursors in ancestral hominins would likely have been marginal. The effect would also be coarse. What goes the last mile in humans is that we can tap into the role model's own understanding via adaptations for teaching and pedagogy (e.g., Csibra and Gergely, 2011; Gärdenfors and Högberg 2017; Tehrani and Riede, 2008), but these abilities are also highly derived, and perhaps to some extent even culturally evolved themselves (see Heyes, 2018, 2021), so functional versions of them also appear unlikely in apelike hominins.

Finally we should ask whether Oldowan hominins may have surprised us by being significantly more cognitively advanced than their brain size and artefacts suggest. Recent evidence do not support such a suspicion. *Homo* retained an ancestral and apelike brain organisation until circa 1.5 Mya (Ponce de León et al., 2021), and the earliest Oldowan artefacts have recently been pushed even further back in time to circa 2.9 Mya, and is even tentatively attributed to (non-ancestral) *Paranthropus* (Plummer et al., 2023).

In summary, while humans can copy know-how that is much more complex and sophisticated than they can produce themselves (on "cultural islands"; Tennie et al., 2016; Tomasello, 1999), the situation is exactly the opposite in extant apes, and it probably also was in our early ancestors. Know-how copying is not only hard to perform, but also of limited use unless supported by additional mechanisms, such as for improved fidelity and abilities for choosing what to copy. Know-how copying in the Oldowan hominins would thereby most likely be inadequate for cumulative culture and face what we called a start-up problem (Fig. 2B). We will later also question whether cumulative know-how would even be particularly adaptive in a simple and apelike setting.

Oldowan know-how copying is *less needed* than widely assumed. Recent studies contradict the widely held idea that Oldowan tools are substantially beyond the abilities of extant toolmaking non-human primates. For example, experimental work by Snyder et al. (2022) shows that Oldowan techniques (and artefacts) can be re-invented on the spot in their entirety, absent know-how models. All Oldowan techniques were spontaneously re-invented by naive human subjects, who had not been told about these skills, had not seen them, and could not reverse engineer them (no Oldowan-like artefacts were provided). Unintentional production (see e.g., Motes-Rodrigo et al., 2022; Proffitt et al., 2016, 2023) and later use (see Westergaard and Suomi, 1995) of sharp flakes has been reported in extant primates, which demonstrates that the potential for such tools was likely clear if pre-Oldowan hominins used stone tools for percussion (which they likely did, see J. C. Thompson et al., 2019). The step to intentional production would likely be short if we assume a motivating need for sharp stone tools and possibly a slightly higher cognitive capacity in Oldowan hominins than in extant apes. Access to fleshed carcasses would provide the former and the latter is a reasonable assumption (Toth and Schick, 2018).

In summary, while it remains somewhat unclear whether extant apes could (and would) invent and produce Oldowan tools, it has become clear that their abilities are not far behind what would be required. That Oldowan toolmakers are likely to have had a *quantitatively* somewhat higher (e.g., Toth and Schick, 2018), yet *qualitatively* similar (Ponce de León et al., 2021), cognitive capacity compared to extant apes seems consistent with such a level and sort of inventive capability. What we see is thereby consistent with a scenario where cultural transmission in Oldowan toolmakers remained apelike (i.e., at the most marginal know-how copying) and based on a possibly slightly better ability for re-invention.

Oldowan know-how copying is *less supported* than widely assumed. The point of our argument is not to rule out the possibility of Oldowan know-how copying. The reason we give it a hard time is to argue that the high prior likelihood that many attach to its presence should be much reduced. If we do, we will thereby be more motivated to *require empirical evidence to accept its presence* (i.e., to "reverse the null hypothesis", see Tennie et al., 2016, 2017). As we shall see, evidence of know-how copying becomes conclusive only *considerably* after the Oldowan.

If know-how copying was used in Oldowan toolmaking, then evidence to support its presence remains to be found. Past the Oldowan, traces of a new technological phase appears around 1.75 Mya with "large cutting tools" that offered more efficient cutting edges than the simple Oldowan flakes and cores (e.g., Diez-Martín et al., 2015). These include the famous bifacially worked Acheulean handaxes. For our purposes, let us divide the impressive tenure of these tools into three rough sub-phases (inspired by Kuhn, 2020, pp. 174–188): *Early Acheulean tools* (circa 1.75–1.0 Mya) have the familiar and enigmatic drop-shaped form but were crudely produced by simple bifacial trimming along the margin. This means they were not subject to the stronger shape control seen in *mature Acheulean tools* (circa 1.0–0.5 Mya) produced using "true bifacial thinning", which is an added technique whereby thinner flakes are removed to regulate not only the width but also the thickness of the core. Finally, as we get closer to the prepared core technologies of the Middle Palaeolithic/Middle Stone Age (MP/MSA; circa 0.3 Mya, where know-how copying can be more confidently deemed as fully established), there was a *transitional Acheulean* period (circa 0.5–0.3 Mya), which saw a radiation of new methods for blank production (flakes for subsequent specialisation), alongside bifaces, foreboding the MP/MSA.

What we see can be described as a trend toward "imposed form" in tool production, going from *definitely absent* at the Oldowan outset to *definitely established* in MP/MSA technology. However, while an ability to copy forms is certainly novel, *form is still not necessarily know-how* (as Tennie, 2023 lays out), and many have indeed raised doubts that large cutting tools indicate any dependence on know-how copying (e.g., Acerbi and Tennie, 2016; Corbey et al., 2016; Snyder et al., 2022; Tennie et al., 2016, 2017; Vaesen and Houkes, 2020). It is also quite plausible that if a selection pressure for more complex technology could not produce know-how copying (due to the "start-up problem"; see Fig. 2B) it could still have yielded *other* adaptive responses, such as an expanded individual ability to re-invent and plan (including hierarchical planning).

The exceptional historical and geographical uniformity of forms and production methods in early Acheulean tools may therefore be parsimoniously explained via equifinality in re-invention, which would only increase if form was copied along with function (further narrowing the search space of invention). The case for know-how copying then *strengthens* when more sophisticated processes for imposing the form emerge in mature Acheulean toolmaking, although we must also factor in the potential that increased brain-based capacities for invention and motor skills may also have produced such an effect (apart from brain expansion, a derived and more humanlike brain architecture appears after circa 1.5 Mya; see Ponce de León et al., 2021). The burden of evidence is more convincingly filled by what we have called the transitional Acheulean some 0.5 Mya (Snyder et al., 2022; Tennie, Bandini et al., 2020; Tennie et al., 2017), where an early example may be production techniques at the Acheulean site of Boxgrove, England (0.5 Mya) where inferred, special techniques with (sometimes specially prepared) organic hammers (but also, often, the stone-tool products) have been suggested as evidence for underlying know-how copying (Roberts and Parfitt, 2015 as cited by Putt et al., 2022). Also foreboding the MP/MSA, the earliest evidence of multi-component implements (hafted spear tips) have been reported from the same general time period (e.g., Wilkins et al., 2012), which likewise strengthens the case for know-how copying and some degree of cumulativity in cultural traits at this time.

Oldowan cumulativity is dead, long live Oldowan cumulativity!. Unless these dilemmas are solved (which we currently deem unlikely) we must conclude that Oldowan know-how copying is neither *likely*, *needed*, nor *supported* by empirical evidence. In fact, *Homo* probably stayed with an ancestral and apelike basic mechanism for cultural transmission for good parts of the Lower Palaeolithic (see Fig. 1 and Snyder et al., 2022; Tennie et al., 2020). Know-how copying appears to be robustly detectable as late as between 1.0 Mya and 0.5 Mya (or perhaps even later, although later dates become more and more unlikely), but may of course have begun to enter gradually at some earlier point in time.

But for this conclusion to appear even the least satisfying we clearly need some other explanation for the much more robust *overall* empirical picture, which tells us that both *Homo* and her cultural behaviour went from apelike to more humanlike forms, roughly from the Oldowan and onward. We now move to introducing our alternative Trajectory B. We first set up the *organisation* of culture under Trajectory B, moving then to its special type of cumulative *evolution*.

Cultural organisation under Trajectory B

According to Trajectory A, human culture took off when know-how copying appeared as a boost to the pre-existing channel of ape-like social cultural transmission. The analysis thereby remains moored to the level of the units and processes we find in ape culture, and a focus on cultural knowledge *within* the brains of individual learners. Trajectory B begins from the same level and units but sees the origin and evolution of human culture as fundamentally about the emergence of *new* types of cultural units and processes across levels of organisation and selection. Cultural organisation *between* learners is therefore particularly salient under Trajectory B, which raises new questions about what the units are, how they evolved, how they interact, and what processes that operate on them.

We begin by investigating the potential that adaptive networks of non-cumulative cultural traits would form ahead of the transition. From these networks, as the proto-units of human culture on the group level, we move to the derived units that we foresee would appear along Trajectory B, introducing terminology to conceptualise this space of cultural organisation between rather than within learners.

The Zone of Latent Solutions. Cumulative know-how may be conceptualised on the background of the "Zone of Latent Solutions" (ZLS; see Tennie et al., 2009; Tennie et al., 2020), which denotes the imagined space of know-how that members of some species can invent individually if basic conditions hold (e.g., they must be properly motivated).[4] If cultural transmission lacks adequate know-how copying, it must rely on (re-)invention of know-how, and the know-how of cultural traits will automatically remain within the ZLS. By contrast, and under additional conditions (see *Oldowan know-how copying is less likely than widely assumed*) know-how copying can avoid this bottleneck (wholly or partly) to sustain cumulative know-how (Tennie et al., 2020) beyond the boundaries of the ZLS.[5] The concept of cumulative know-how can also be further specified in this context as *copying-dependent* to stress its dependence on cultural models, and *supraindividual* to stress that it cannot be invented by single individuals (see Tennie, 2023). However, we have argued that human cumulative culture originated considerably *before* such an exit from the ZLS became realistic.

Trajectory B proposes that the roots of human culture lie in an unforeseen type of cumulative culture that may arise, persist, and grow *within* the realm of the ZLS. The cultural knowledge that undergoes cumulative cultural evolution is in this case not in the cultural traits as such, but in the structure of *interactions* between non-cumulative cultural traits. Hints of such a subspace of the ZLS have been noted and described as a "grey-zone of cumulative culture" (Tennie et al., 2020) with unusually large units of know-how that can be invented by daisy-chaining *re-inventable elements* of know-how. We will now describe this grey-zone and—importantly—extend it since it presently applies only to know-how linkages *within* single individuals.

Extending the grey-zone of cumulative culture. Cultural traits in the grey-zone are underpinned by know-how that on first sight may *appear* to be cumulative. Tennie et al. (2020) describe cases where elements of know-how are individually invented by a single individual in a sequence *where each element primes the learner to invent the next*. This describes a re-entrant version of ape-style cultural transmission, as illustrated in Fig. 1. The whole unit of know-how may then become too complex and/or opaque for apes to invent in one go. This may trick an observer to believe that the know-how is cumulative, and either that know-how copying must thereby have taken place, or that cumulative know-how is possible without know-how copying. Empirical cases of grey-zone culture remain to be properly described in *Pan*, but candidate examples include nut-cracking using hammerstone and transported anvil.

Let us generalise this re-entrant twist on invention: The grey-zone arises because learning *one* unit of know-how can prime the learning of a *different* unit of know-how, and because these units *together* can offer adaptive *emergent* functionality, above and beyond what the units provide on their own. We now observe that no obvious reasons prevent such linkages from forming also between different cultural traits practiced by *different* individuals, potentially even at different times and places.

Networks of cultural traits may thereby be possible. We propose that linkages can form if the *functions* of cultural traits are copied, which apes indeed do. Apes copy the know-what, know-where, know-why, and so on, of cultural traits to constrain and direct their inventive capacity to resupply the know-how needed to satisfy those constraints. *Doing that is tantamount to copying the function of the cultural trait* since the transmitted trait still does the same thing, such as cracking a nut in some particular setting. The persistence observed in some cultural traits of apes also shows us that the fidelity of this "ape function copying" can be quite high (e.g., Mercader et al., 2007, 2002). Now, if the function of a cultural trait is dependent on the function of *another* cultural trait, we may see this as a link in a network of cultural traits. For example, if one cultural trait leads to rocks of some particular quality or shape becoming frequent, and another trait produces tools using those newly available rocks, then these two traits are linked regardless of whether they were produced by the same ape or not. Copying the functions of linked cultural traits will therefore maintain such links, and thereby also elements of *network structure* (see also Buskell et al., 2019 for a pertaining discussion about linking cultural traits).

How could such networks arise? The persistent presence of some cultural function in a community may modify the local learning environment so that an additional function can be invented and linked to it, for instance via the use of its products or by-products, or by adding or modifying a factor that it uses. Such combinations may have emergent effects that are different than those of the linked cultural traits individually, and those (possibly adaptive) effects will arise whether or not the learners are aware of them or not. This will again modify the learning environment, maybe enabling a third link, and a fourth, and so on, growing the network. Since the ability to understand and be motivated to learn by such links would be highly limited in an apelike hominin, it is important to stress that *such links can also form via side-effects* of some primary function that motivates the learner to learn and use it. For example, percussive stone-tool use could produce sharp flakes as a side-effect and thereby produce a link to a second cultural trait where those sharp flakes were put to use (compare Carvalho et al., 2008).

The territorial and tightly socially integrated social organisation of chimpanzees, which is likely to have been shared in outline by our early hominin ancestors (discussed in more detail below), appears to favour the formation of such networks (provided they are possible), since it will keep apes, activities, and material effects persistently in close proximity. Cultural traits in chimpanzees and humans have indeed been shown to exhibit a highly non-random nested distribution across social communities, meaning that different cultural traits may not only be stable as such, but also remain *together* over prolonged periods of time (Kamilar and Atkinson, 2014; Lycett et al., 2009).

Such systems could potentially arise in contexts mediated by "ecological inheritance" (Odling-Smee et al., 2003), such as chimpanzee nut-cracking sites that are formed and maintained by selective transportation and use of hammerstones and anvils, and may be highly persistent (verifiably across over two hundred generations, see Mercader et al., 2002, 2007). Regardless of whether, and the extent to which, the different know-how aspects (e.g., schlepping stones and cracking nuts) are (or must be) socially learned in this particular example, it still demonstrates how ape behaviours can produce distributed, self-organised and persistent behavioural networks with emergent problem-solving effects (e.g., Carvalho et al., 2008). In this case, the nut-cracking behavioural network modifies the behaviour of the apes directly and indirectly, for example by concentrating tools and raw materials, by producing new learning opportunities, and as an arena for the formation of synergies between behaviors (arising as attractors in dynamical systems when individuals ongoingly and mutually adjust their behaviours to improve returns; see Keenan and McShea 2023). Such self-organised cultural complexity can be based on quite simple behaviours, but is easily misdiagnosed as the outcome of strategical planning (Luncz et al., 2016).

Another candidate situation could be chimpanzee border patrols, which emerge from a complex fabric of fast and dynamically interlinked activities that are distributed both socially and geographically (see e.g., Amsler, 2010; Wrangham and Glowacki, 2012). While we cannot be sure that border patrols actually include any culturally transmitted components,[6] they do produce situations that appear conducive for cultural transmission since they align the behaviour of groups of apes (socially and repeatedly). Collective hunting behaviour (see e.g., Hobaiter et al., 2017) could be yet another example.

We refer to the grey-zone in its original sense as the *intensive* grey-zone since the know-how here expands *within* the brain of a single individual (e.g., a complex method for nut-cracking). In the extended version of the grey-zone, culture expands instead via networking of cultural traits *between* different individuals (and across space and time), and we label this the *extensive* grey-zone. Our potential examples of networks in the extensive grey-zone must be examined in higher detail, but, even under the constraints of limited abilities to understand and be motivated to learn by synergies between cultural traits, their possibility as animal cultural phenomena should be taken seriously, not least via side-effect linkage.

Institutions and cultural idea systems. We will refer to networks in the extensive grey-zone as *proto-institutions* that would work as seeds of the cumulative *institutions* that we propose arose along Trajectory B. An institution in this sense is a nameable domain of cultural activity that integrates functions of cultural traits to produce an emergent cultural function, such as hunting, cooking, marriage, or childcare. Institutional units can in turn be linked and nested to produce what we speak of as *cultural idea systems* that are maintained and contained within social communities (Leaf and Read, 2012; Read, 2012; Read and Andersson, 2019; Voorhees et al., 2020).

We use the term institution broadly to emphasise the structuring effects that such networks have on patterns of behaviour and cognition, regardless of whether those are side-effects or primary functions, and regardless of whether the networks specifically consist of norms and rules (the latter, which is what is usually meant by "institution", are specialised later forms that require derived capabilities; see e.g., Powers et al., 2016). The evolution of institutional organisation is covered in the next section, and we propose that pre-Oldowan carnivory (see e.g., Pobiner, 2020; Thompson et al., 2019) during the Pliocene could have been the target of the original institution around which the cultural idea systems of *Homo* took shape.

Intensive vs. extensive culture. We will use the terms *extensive* and *intensive* to generally differentiate between cultural organisation that, respectively, extends *between* and *within* individual learners. This also permits us to speak of dimensions and levels of cultural organisation as intensive or extensive (potentially with many levels within). The main point of making this distinction is that *distinctly different sets of processes operate on the extensive and intensive levels of culture*. Perhaps most saliently, the intensive-level channel of inheritance is cultural transmission between individuals, while the extensive-level channel of inheritance is a social group-level process (described in more detail in the next section).

Speaking of an extensive and an intensive dimension of culture also permits us to expediently indicate the level we intend theoretical concepts to apply to (e.g., cumulativity, know-how, and so on), including not least for asking what concepts that are familiar in their intensive incarnation could mean on the extensive level. For example, *intensive cumulativity* applies to cultural traits, and *extensive cumulativity* to networks of cultural traits, such as institutions and higher-order systems thereof (see Fig. 3).

To simplify the terminology, we will preserve the term *cultural trait* for the intensive level and refer to what may have been called "extensive cultural traits" as *proto-institutions* and *institutions*. We then differentiate between *latent* and *cumulative* cultural traits to indicate whether they are, respectively, inside or outside the Zone of Latent Solutions (i.e., copying-dependent, or not). Examples of cumulative cultural traits could include, for example, the skill of producing a late type of specialised stone-tool (e.g., an arrowhead).

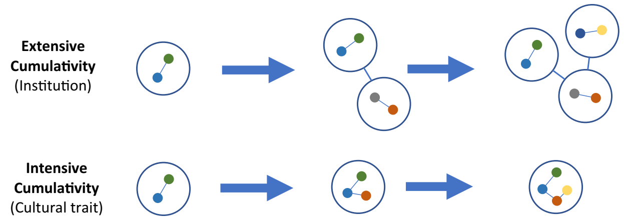


Fig. 3 Cumulativity on two levels. *Extensive cumulativity* is the cumulative evolution of cultural organisation *between* individual learners. *Intensive cumulativity* is the cumulative evolution of cultural organisation *within* individual learners. The former builds emergent higher-level functional systems that we refer to as *institutions*, while the latter builds *cultural traits*. The two modes are combined in human culture but are based on different processes and thereby do not strictly imply or demand one another and may have appeared at separate times in human pre-history.

Early institutions. As a potential example of an early institution, Davison et al. (2021) infers the “Oldowan Carnivory Institution” as a minimal network of complementary cultural traits required for Oldowan toolmaking to serve the function we usually attribute to it in hominin carnivory. Suitable pebbles would need to be *selected and transported* and then used for *producing* sharp flakes. Fleshed carcasses had to be *found* and *defended*, and the sharp flakes had to be skilfully used to *process* them into consumable forms. What sticks out here is not that the function would require particularly sophisticated know-how (they may well all be latent know-how). What sticks out is how they are networked and interdependent across temporal, spatial, and social spaces. For example, if fleshed carcasses are not secured, sharp tools are not needed, which makes the collection of suitable pebbles pointless. If suitable pebbles are not collected, tools cannot be made, and fleshed carcasses will be much less useful. This sticks out as a departure from apelike to humanlike organisation of culture as an expansion of the extensive dimension.

Extensive cumulativity may have come first. Even if modern human culture is cumulative in *both* the extensive and the intensive dimensions, there is no obvious reason why that has to be the case. We could imagine highly cumulative cultural traits with no interactions between them, and we could also imagine apelike latent cultural traits networked into cumulative institutional units. This implies that extensive cumulativity *could have appeared before intensive cumulativity*. This is what Trajectory B suggests happened since the potential for extensive cumulativity does not appear to rely on the presence of special cognitive capabilities. Trajectory B also proposes that extensive cumulativity *produced the conditions under which intensive cumulativity became likely and needed at a later point in time* when it is also supported by direct empirical evidence.

We now move to the question of how these group-level units of extensive culture would have come under natural selection and cumulative evolution.

Cultural evolution under Trajectory B

The impasse of Trajectory A may also be understood as a failure to account for cultural traits as effective *units of selection* (Lewontin, 1970; Sober and Wilson, 1994) capable of adapting on the intensive level until long past the Oldowan. Trajectory B seeks to avoid this problem by instead accounting for a group-level cultural unit of selection on the extensive level, potentially arising even earlier than the Oldowan.

***Being* a cultural unit of selection**. The capacity of groups to undergo evolution by natural selection as wholes can been conceptualised as their degree of *evolutionary individuality* (see Buss, 1987; Michod, 1999; Radzvilavicius and Blackstone, 2018). Groups with a high degree of evolutionary individuality may then simply be referred to as *units of selection* that exhibit phenotypic variation, differential fitness, and heritable fitness (Lewontin, 1970). Biological organisms are emblematic examples, but their ranks also contain cases that remind us that recognising units of selection is harder than it may seem. For example, while termites clearly are organisms, they are *no longer* units of selection. They turned into parts of their colonies when cooperative groups of termites underwent an *Evolutionary Transition in Individuality* (e.g., Clarke, 2014; Hanschen et al., 2015; Maynard-Smith and Szathmáry, 1995; Michod, 1999, 2007; Szathmáry, 2015). It is now *colonies as wholes* that have the features of a unit of selection, which has turned them into a highly unusual type of organism that challenges deeply seated notions about what organisms and units of selection should look like (e.g., Boomsma and Gawne, 2018; Kennedy et al., 2017).

Since intuition clearly is a feeble guide, our assessments of evolutionary individuality must be based on more objective insights instead. For example, about what natural selection requires to operate, and about tell-tale features that only units of selection would exhibit. To illustrate, let us first see how such questions may be answered on the more familiar intensive level, which is to say for cultural traits.

To do this, let us cursorily apply some criteria developed for assessing evolutionary individuality (see Davison et al., 2021). We may easily convince ourselves that even apelike (latent) cultural traits have lifecycles with distinct beginnings and ends (learning and death), and that they are individuated as systems of know-how under a common function and motivation (such as cracking a nut). They may also be imagined as reproducing via cultural transmission, which means they can spread and form populations in a substrate of socially linked learners. *Their problem is inheritance*. Since their know-how must be re-invented each lifecycle, they can be units of selection only to the marginal extent permitted by their faithfully copied functions (see *Extending the grey-zone of cumulative culture*). This also explains all the focus on know-how copying. If latent cultural traits only had know-how copying, there would be a case for them as adequate units of selection capable of undergoing cumulative cultural evolution.

It is today commonplace to subscribe to some argument that human (cumulative) cultural traits are units of selection, and the idea is even spread in the public imaginary as “memes” (coined by Dawkins, 1976)—so widespread that it is often remarked that the idea is an excellent example of itself. As we have seen, Trajectory A is also firmly based on such a view. It views animal cultural traits, and in particular those of apes, as pre-adapted for *becoming* units of selection and know-how copying as the final missing piece of the puzzle (e.g., Whiten et al., 1999).

***Becoming* a cultural unit of selection**. We now shift to the question of how units can *gain* evolutionary individuality. The key insight is that evolutionary individuality *itself* is an adaptation that can evolve like any other adaptation (Buss, 1987). This is easy to overlook since even if the mechanisms that high evolutionary individuality (e.g., chromosome replication, meiosis, multicellular development, etc.) to mature units of selection (like in animals, plants, bacteria, etc.) are highly complex and sophisticated, they do not vary much at all today, and they undergo very little evolutionary change. The reason is that they were settled on as solutions at an early point and were (since very long ago) refined to a degree where almost no adaptive variation remains (they are firmly generatively entrenched, see Wimsatt, 1986), and may thereby now appear more like the immutable conditions for evolution than like traits that evolve in their own right. Natural selection may act almost entirely conservatively on these traits, but that is not to say *weakly*. To the contrary, maintaining such exceptionally complex and delicate adaptations demands relentless selection pressures for the functions and level of performance that they deliver. Early on, before this refinement and entrenchment, these selection pressures had adaptive variation to work on, and the exploration of improvements would be a major area of evolutionary action. Increased evolutionary individuality is key to all evolutionary adaptation (a larger evolutionary "design space"; see Stankiewicz, 2000) including, as we shall see, *the adaptation of evolutionary individuality itself*.

Returning to latent cultural traits (such as in apes), we referred to these as *marginal* units of selection since their evolutionary individuality is highly limited. We also described them as *attractive* as potential origins of true units of selection since they lack only one single factor to become quite effective units of selection, namely faithful know-how copying. Cultural traits cannot, however, gain know-how copying *themselves* via evolution since all their features and processes are externally provided via their learners. This complicates the evolutionary picture since it does not matter if strong selection pressures favour the evolution of faithful know-how copying *in the latent trait*—it has to be adaptive *for the learners*, which are separate and mature units of selection. Provisioning faithful know-how copying may of course be in the fitness interests of apes, but we argued that this is not likely to have happened (both empirically and theoretically) until considerably later than most presume (see *Trajectory A at an impasse*).

What about the *extensive* cultural units we have discussed so far? Proto-institutions actually look much less like they would be on the verge of becoming units of selection. Institutions are neither learned nor expressed as wholes and we described them as standing self-organised behavioural patterns (see *Extending the grey-zone of cumulative culture*). If we tried to account for a lifecycle, with reproduction, birth-and-death, and so on, the story would be considerably more laboured than the one for latent cultural traits (see *Being a cultural unit of selection*).

The extensive unit that we argue *is* on the verge of becoming a unit of selection is, however, not the institution, but *the cultural idea system as a whole*, which is to say all things cultural within the social bounds of communities. To see the cultural idea system as an incipient unit of selection we have to zoom out from the Trajectory-A-imposed focus on the level of cultural traits and their transmission. As we do, social behaviours, ecology, and dynamics spanning across many generations of hominins and cultural traits come into view (including cultural trait transmission). As a unit of selection, we refer to the cultural idea system as a *sociont* to delineate it from the co-extensive hominin community, which serves as its substrate (see Andersson and Törnberg, 2019; Davison et al., 2021). The sociont and the cultural idea system are in other words the same thing—but seen from an evolutionary and a hominin perspective, respectively.

Like the cultural trait, the sociont is also seen as arising from a primordial pre-adapted unit that lacks only one single piece to become a unit of selection. What is missing here is, however, as we will see, not faithful inheritance but merely an ecological factor that corresponds well to what Pliocene hominin carnivory offered (which most agree indeed appeared in this time frame). We will also argue that the sociont has considerably more potent affordances than the cultural trait for gaining evolutionary individuality via natural selection acting directly on itself.

One could think that new units of selection would evolve frequently given the strength we attributed to the selection pressures favouring evolutionary individuality. However, selection pressures are without consequence unless they operate on units that *already* have sufficient evolutionary individuality to adapt in response to them. This brings us back to the start-up problem depicted in Fig. 2. We hereby turn to the *origin* of units of selection. How do pre-adapted units of selection arise, what must we require of them, and how must evolution act on them to turn them into new units of selection, such as multicellular eukaryotes, termite colonies, or, in this case, the sociont?

Evolutionary Transitions in Individuality. ETI is a well-known and accepted type of evolutionary pathway that produces new units of selection by combining existing ones (see *Being a cultural unit of selection*). It is via ETI's that cooperative groups of prokaryotes gave rise to unicellular eukaryotes, then to many types of multicellular eukaryotes (such as plants, animals, and fungi), and finally to eusocial insect colonies (such as ants and termites). Notably, ETI's are the main (perhaps the only) unequivocal architects of higher complexity in life (e.g., Carmel and Shavit, 2020; Marcot and McShea, 2007).

An ETI may be approximated as a rare type of self-reinforcing group selection.[7] Essentially, since group selection affords group-level adaptations, and since evolutionary individuality is an adaptation, group selection may *under fortuitous conditions* lead to improvements of the group's capacity for undergoing group selection. Fundamentally, the evolutionary individuality of the group increases as it adapts to *reduce* the evolutionary individuality of its members (fitness is "exported" upwards; see Michod and Herron, 2006; Michod, 2007). This is because the higher the evolutionary individuality of the members is, the better they are at following *their own* fitness interests when they conflict with those of the group, which is frequently referred to as *cheating* in the literature. Suppressing their ability or incentive to cheat thereby means that some group-level adaptations that used to be undermined by cheating now become stable, and that the group thereby increases its ability to adapt according to *its* fitness interests.

Since the selection pressures favouring evolutionary individuality would be strong, some of the adaptive freedom gained by removing cheating opportunities would (if possible) be well invested increasing the group units' evolutionary individuality even further, increasing thereby the adaptive capacity even more on the group level. Not least, the more closely the group members cooperate and specialise in *internal* functions of group, the more they would lose adaptations for an independent life (in evolutionary trade-offs and reduced selection pressures). Our examples of ETIs above all ended in a nearly total "victory" for the group. For example, our body cells once were free-living unicellular eukaryotes (choanoflagellates), but are now wholly unable to survive and reproduce at all on their own. Cheating is therefore no longer feasible. As an ETI progresses we get less inclined to speak of groups and members and more inclined to speak of units composed by proper parts such as cells, organelles, *or*, in our case here, *cultural traits*.

Group selection does not typically end up this way, however. To undergo an ETI, a group must arise with a fortuitously pre-adapted set of key features that provide it with evolutionary individuality from the outset, such as individuation, reproduction, and inheritance. This means that the pre-conditions for an ETI must appear for other adaptive reasons, which is also why ETI's happen only rarely (see e.g., Clarke, 2014). Evolution cannot search for an ETI—it must stumble upon it. We refer to the fortuitous set of circumstances that we argue provided the sociont with such features as "the social protocell".

The Social Protocell Hypothesis. To account for the origin and evolution of evolutionary individuality on the extensive level, we now introduce the Social Protocell Hypothesis (Andersson and Czárán, 2023; Andersson and Törnberg, 2019; Davison et al., 2021), which argues that the fortuitous conditions required for an ETI arose in the hominin lineage, and are mostly present also in our closest relatives in *Pan*. In a nutshell, the social communities of *Pan* and early hominins are proposed to act as growing and dividing compartments for latent cultural traits, and thereby impart individuation, reproduction, and inheritance to their cultural contents as wholes. This would have constituted the primordial sociont and enabled its cumulative evolution of extensive-level cultural idea systems by providing a sufficient degree of evolutionary individuality to enter the positive feedback loop of an ETI.

Note that the setting we just described closely resembles the conditions believed to be responsible for the origin of cellular life via an ETI (Gánti, 1975; Michod, 1983; Norris and Raine, 1998; Szathmáry and Demeter, 1987; Szathmáry and Maynard-Smith, 1995). This parallel provides us with detailed theoretical tools for exploring the origin and evolution of culture under Trajectory B. For other applications of ETI and similar concepts to human culture, see e.g., Carmel et al., 2023; Grey and Watts, 2017, review by Waring and Wood, 2021, and also McShea (2023) for a critique that notably exempts the Social Protocell Hypothesis since it specifically targets the main theme of other cultural ETI applications, namely social groups of *humans* undergoing a *recent* ETI. Let us first illustrate the principles of the protocell in its original context before we move to its proposed re-appearance in a cultural setting (see Fig. 4).

The biotic protocell plays a key role in explaining the transition from metabolic networks of separately reproducing RNA protogenes to simple cellular forms of life. The idea is that RNA-based metabolic networks came to produce (as a by-product) amphiphilic lipids that self-organised into vesicles that enclosed the RNA networks within themselves. As lipids and RNA copies were produced within these vesicles, they would grow and eventually destabilise to split into two daughter vesicles. This automatically divides the chemical contents of the parent vesicle, with each daughter vesicle receiving on average the same mix of protogenes as the parent vesicle. In this way a coincidental by-product of the evolution of protogenetic networks could just happen to provide individuation, reproduction, and inheritance on the level of groups of metabolic networks of protogenes.

The more efficiently the inherited metabolic RNA-based networks produced new copies of themselves, producing vesicle lipids as they went along, the faster the protocell would produce copies of itself as a whole. Evolution could thereby produce increasingly adaptive protocells via selection for variants with more adaptive metabolic networks.

The potential for self-reinforcing evolution of evolutionary individuality is quite clear. Chemical compounds produced by the metabolic networks would be heritable and able to modify chemical reactions in the metabolic networks as well as in the membrane. For example, to make the protocells more cohesive, larger, splitting more symmetrically, and so on. In this way, a coincidental group-level unit of selection could embark on a gradual evolutionary trajectory to become a specialised unit of selection—specifically a prokaryotic cell. The outcome can be seen in the *much* more sophisticated membrane, division, and genome replication mechanisms in prokaryotes, whose basic solutions have remained entrenched ever since (e.g., Maynard-Smith and Szathmáry, 1993).

We will now outline *the social protocell* before going into its mechanisms in more detail. It is based on the growth-and-fission lifecycle of social communities that may be observed in *Pan* today (see e.g., Feldblum et al., 2018; Furuichi 1987; Langergraber et al., 2014; Moffett, 2013), and that we have reasons to believe was likely present in a similar form in the last common ancestor between *Homo* and *Pan* some 57 Mya (Kumar et al., 2005). The reasons include that chimpanzees appear to have changed little in general to this day, neither in terms of habitat or anatomy (see Pilbeam and Lieberman, 2017), and that human groups on the corresponding level (sometimes referred to as *clans* in the literature) have similar cohesion mechanisms and similarly undergo fission along conflictual fault lines (e.g., Chaix et al., 2004; Hart and van Vugt, 2006; Moffett, 2013). Overall, the picture is consistent with the idea that human group behaviour evolved from a chimpanzee-like starting point (see also Grove et al., 2012; Layton et al., 2012). So while the *internal* organisation of *Homo* communities has changed (such as pair bonding; see Gavrilets, 2012, and additional levels of internal organisation; see Grove et al., 2012), the envelope features that the

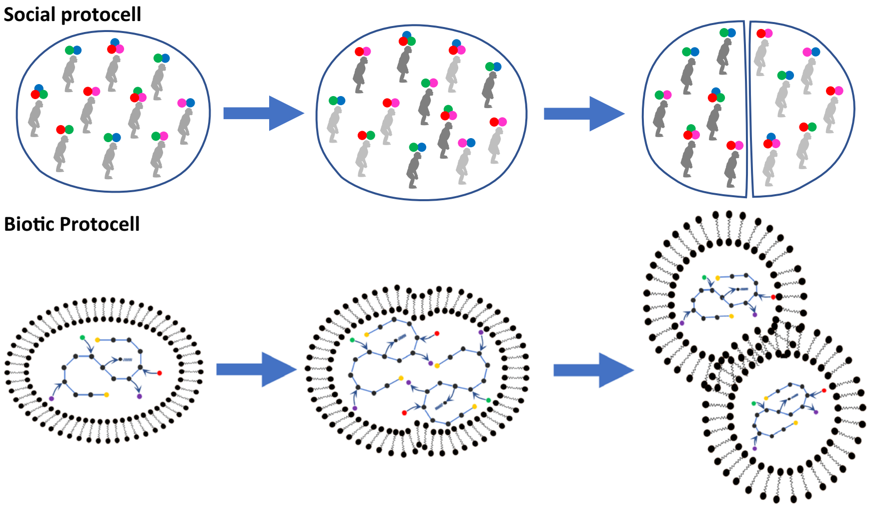


Fig. 4 Protocells. In the illustration of the social protocell (top), the hue represents diverging social identity and a social fault line ahead of the community split. The coloured circles represent different types of latent cultural traits. In the biotic protocell illustration (bottom), a lipid vesicle is produced by a metabolic network of different protogenetic (RNA) components. In both cases, the dynamic causes growth and division of containers of information, where the proportions of the contained information will be similar in parent and daughter communities in the group-level lifecycle that results.

social protocell is based on appear to have persisted, with the community/clan likely remaining the top level of social organisation to the end of the Middle Palaeolithic/Middle Stone Age (see Layton et al., 2012).

The social protocell provides *individuation* via a membrane-equivalent that may be described as a social rather than chemical vesicle. Its effects are highly similar and just as real. While the biotic protocell keeps its lower-level units inside and in close contact by physically blocking their passage, the social protocell does the same by *socially* blocking the passage of cultural traits. The mechanism is the *much* lower intensity of social links between individuals in different communities compared with between individuals within the same community.[8] Consider how the factors that van Boekholt et al. (2021) cite as premiering high rates of social learning (e.g., social tolerance and bonding) are maximised *within* social communities but minimised *between* them; see also Tostevin (2007).

Reproduction is provided via irreversible community-level fission whereby parent communities divide into daughter communities as a result of runaway polarisation via conflicts (not to be confused with the ongoing fission and fusion of foraging groups within the community). Community fission hereby also provides extensive cultural *inheritance* by splitting the social hominin substrate of the cultural traits in *two statistically similar extensive cultural units*. The rate of irreversible community fission has been argued to increase as population growth strains social reconciliation mechanisms (Aiello and Dunbar, 1993; Langergraber et al., 2014; Moffett, 2013; Sueur et al., 2011). Socionts that improve the fitness of the hominins maintaining them would then potentially encroach on neighbour socionts, divide more frequently, and spread at the expense of less competitive socionts (Andersson and Czárán, 2023).

Culture governs behaviour, and since the sociont *is* a cumulative cultural idea system from the perspective of the hominin, it will be ideally positioned to culturally adapt hominin behaviour *also to increase its evolutionary individuality*, which we will return to repeatedly below.

We have hereby outlined the sociont as the unit of selection within which cumulative extensive culture is proposed to have evolved under Trajectory B (see Davison et al., 2021 for an application of a battery of criteria for evolutionary individuality to the sociont). Like the biotic protocell, the appearance of the social protocell is entirely fortuitous and based on social group behaviour whose evolution can be accounted for without invoking any of its effects on culture, which itself is a widespread phenomenon. Ape culture can thereby of course also be explained without reference to the social protocell. While the biotic protocell is produced by the proto-genes (and networks thereof) that subsequently undergo the ETI, the social protocell exemplifies what has been referred to as "ecological scaffolding" since its factors are external to the cultural traits' (and their networks') and belong to their environment (see Black et al., 2020; Bourrat 2022).

The inheritance of extensive culture. The social protocell is at bottom a highly simple phenomenon that requires no specialised biological and/or cultural adaptations (see Fig. 5). It effects extensive cultural inheritance via the fact that cultural traits in a parent community are statistically likely to be represented in similar proportions in daughter communities after a split, preserving thereby also the link structure of their networks. Its simplicity and robustness as an inheritance mechanism stems not least from the fact that *nothing on the underlying intensive level gets copied (or even transmitted) in this process*. The hominins just keep doing what they were doing as they are partitioned into two new social communities. This condition is easy to fulfil.

But even if nothing seems to get copied in this process, social protocell inheritance is still *functionally* equivalent to copying on its own emergent level. One instance of a cultural idea system ends up as two thenceforth independent instances, and *the details are preserved* as this happens, which in the extensive case means the functions of cultural traits and the links between

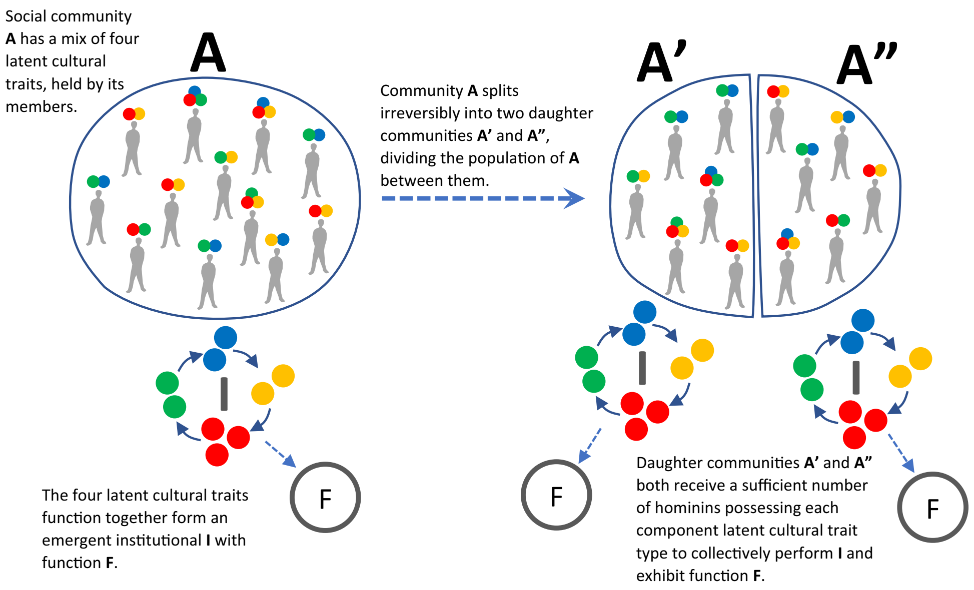


Fig. 5 Inheritance. We here look closer at the hereditary mechanism of the social protocell. Social protocell inheritance arises as an emergent side-effect of social group behaviour and cultural transmission. The community split can be seen as copying the institution **I** even if no intensive know-how gets copied or even transmitted in association with the split. The sociont possesses institution **I** to exhibit function **F**, even if neither the workings of **I** nor the nature of **F** is understood by any of the community members. This process may underpin cumulative evolution of the structure of the process **I**, via selection acting on variation in function **F**.

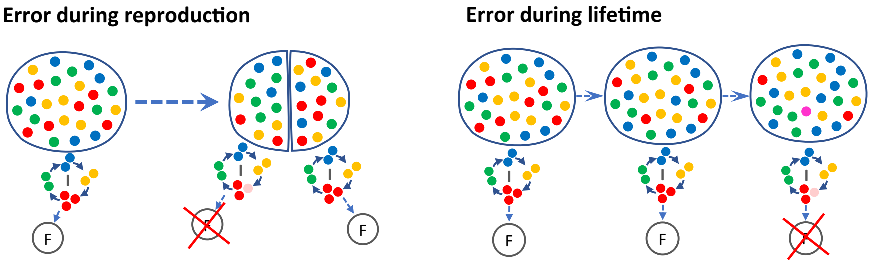


Fig. 6 Errors in transmission. Social protocell fidelity is about maintaining the emergent function **F** of institution **I**, consisting of independently transmitted cultural traits (coloured circles). Two main sources of failure can be readily identified. The first (left) is that too few instances of some traits make it into one of the daughter communities after a split. The second (right) is that traits disappear during the lifetime of a community, due to death and migration. In both cases, fidelity increases if the size of the population increases, and if the components are widely adopted in the group. In reproduction, symmetric splits would be favourable. The cycles depicted as **I** in the figure represent institutions where several cultural trait types (colour coded) must be present at some level for the institution to deliver its function **F**.

them. Variation downstream of a split will modify a specific persisting cultural trait network architecture, which means that it gets applied cumulatively, and that it applies only to its own lineage.

Essentially, the fidelity of social protocell inheritance will be the likelihood that the cultural idea system of the parent is preserved also in the daughter units after a split. Inheritance is thereby adequate for cumulative evolution if *at least a threshold-level number of individuals possessing each of the necessary cultural traits in the parent community end up in each daughter community* (see also Andersson and Czárán, 2023). In Fig. 6 we illustrate how failure to maintain institutional function may arise from loss of cultural traits both during reproduction and during the lifetime of a community. At a low extensive complexity, with maybe a handful of linked traits, possessed by a sizeable proportion of the population, the likelihood that their combined practice as an institution (or proto-institution) will survive a split could certainly be high.[9]

The adaptation of extensive culture. Since the selection of cultural traits is strongly biased by *motivations* for learning (see e.g., *The Zone of Latent Solutions*), apelike ancestral hominins cannot be assumed to have transmitted culture on the basis of adaptive qualities in any general objective sense (which would be exceedingly hard to assess with any confidence). We should only assume they were motivated to learn when they could confidently foresee payoffs to themselves. We argued that this would attenuate selection pressures acting on cumulative cultural traits (see *Oldowan know-how copying is less likely than widely assumed*), and thereby suppress intensive cumulative evolution. However, it would also suppress extensive cumulative evolution, namely by constraining the formation of links between cultural traits.

The reason is that payoffs that are contingent on *other* cultural traits would be indirect, hard to confidently assess, and thereby provide weak motivations for learning in an apelike primordial state. However, while this would likely be *highly* constraining, it would still not suppress extensive cultural evolution in the pernicious way that it does for intensive cumulativity. In the intensive case *selection as such* is suppressed, while in the extensive case the constraint is on variation. This means that as long as *some* adequate design space of extensive culture remains, selection could still operate efficiently since inheritance via the social protocell is not conditioned on any assessments and motivations by learners.

The reason why some extensive cultural design space probably remained despite this strong constraint is that network links can form also via *unintended side effects* of cultural traits that are learned and practiced for *other* primary reasons (see *Extending the grey-zone of cumulative culture*). If cumulative extensive culture gained a persistent foothold and began expanding on such a basis, its presence would shape selection pressures on the hominins, allowing improved abilities to link cultural traits to evolve gradually to, bit by bit, fortify and expand the extensive evolutionary design space.

The selection of extensive culture. The sociont's fitness would vary with heritable cultural variation that affected its relative growth and division rates in populations of sociont individuals. Assuming that early hominins, like *Pan*, defended territories, sociont populations would essentially be tiled on a surface with direct competition between nearest neighbours; see also simulated sociont territorial competition and evolution by Andersson and Czárán (2023), and video links in endnote.[10] Adaptive sociont traits could include for example culturally improved provision, quality and processing of food and other resources, mitigation of environmental risks (dwelling, mobility, storage, and so on), conflict resolution, territorial defence and offence, and so on. But also, and not least, it would also include improvements of the sociont's evolutionary individuality.

How the sociont would improve its own evolutionary individuality is an issue that calls for further dedicated research, but there appears to be an interesting difference between cultural and biological units of selection in this regard that we will now outline and later discuss in some more detail.

As we have discussed, latent cultural traits are highly marginal as units of selection since they lack know-how inheritance (see *Being a cultural unit of selection*). We may now add that apelike learners also select what to learn with a heavy bias shaped by strong limitations in their ability to assess the value of behaviours (see *The adaptation of extensive culture*). On the one hand, this would facilitate an ETI for the sociont since if its group members (latent traits) have a low evolutionary individuality, their fitness conflicts with the group-level unit (sociont) would be fewer and easier to deal with. On the other hand, however, the evolutionary individuality of latent traits seems to be low in the wrong way for facilitating an ETI. The reason is that latent traits not only have a poor ability to cheat, but a poor ability to adapt on their own in general. The sociont would therefore not appear to gain much ability to adapt for itself by gaining control over them. In an ETI, the group-level unit evolutionarily seeks to control its group members in order to *commandeer* their capabilities for achieving highly specific forms and functions, which may be presumed to be quite potent since they enter the ETI as highly evolved separate units of selection.

The twist is that latent cultural traits actually *are* capable of taking on quite specific adapted forms, if only their ape learners can be convinced to *provide them* with the required know-how. Rather than suppressing natural selection of cultural traits, the sociont's main concern during the ETI would on this analysis be to expand and govern the capacity and motivation of hominins to select and furnish know-how to latent cultural traits that were adaptive to the sociont. Know-how copying would here enter as an innovation that drastically expanded the range of possible forms and functions of cultural traits. However, faithful know-how inheritance was also that last missing puzzle piece to turn the latent trait into a cumulative unit of selection (see *Being a cultural unit of selection*). This would give the cultural trait the independent "memetic" ability that Dawkins (1976) described not least as an ability to exploit loopholes in our defences against superfluous and harmful ideas (consider for example suicide cults as an extreme example). From the sociont's perspective, this may have necessitated increased efforts to suppress the selection of cheating cumulative cultural traits at this later point (e.g., via normative systems, which is a topic that will be explored in a forthcoming article).

Finally, to explain why a cultural ETI was triggered in the hominin case but not in the *Pan* case we need to identify a sufficiently adaptive and overall suitable *target* of cultural specialisation that was available to the former but not to the latter. We will return to this question below to explain how pre-Oldowan scavenging in large predator kill sites fits this description well.

Trajectory B from animal to human culture

Figure 7 illustrates how *Trajectory A* begins with the appearance of know-how copying in cultural transmission and thereby intensive cultural cumulativity, which builds up cultural complexity *within* intensive cultural traits. Extensive cultural complexity then increases much later in human pre-history. *Trajectory B* reverses this ordering. Here, faithful cultural inheritance first appears via the social protocell, which builds up extensive cultural complexity *between* latent cultural traits. Here it is know-how copying, and intensive cultural cumulativity, that arises at a much later point.

We now examine three important sub-histories under a possible realisation of Trajectory B. These accounts are scouting expeditions for future in-depth inquiries, and they are unavoidably speculative at this point. Apart from elaborating some key propositions from earlier in the article, they are also meant to principally demonstrate ways in which Trajectory B produces alternative outlooks by *restructuring* existing evidence.

The first expedition examines the question of what the "cultural project" that fuelled the evolution of an incipient sociont via the social protocell could have been. *The second* looks at how the initial sociont could have improved its own evolutionary individuality. *The third* elaborates the proposition that Trajectory B may also explain how and why adequate know-how copying, and thereby intensive cumulativity, emerged at a later point in time. *Finally*, the third enquiry leads us to comment on the fact that Trajectory A notoriously lacks any corresponding analysis of why and how extensive complexity would increase later on in *its* account of human pre-history (see Fig. 7).

The roots of human culture. The Oldowan has a much less archaeologically visible pre-history of simpler forms of hominin carnivory. Its traces are rare and debated, but new finds keep appearing (see e.g., Domínguez-Rodrigo et al., 2010; McPherron et al., 2010; Sandgathe et al., 2011; Thompson et al., 2015). We propose that human cumulative culture took root in the extensive form from spontaneously and intermittently appearing proto-

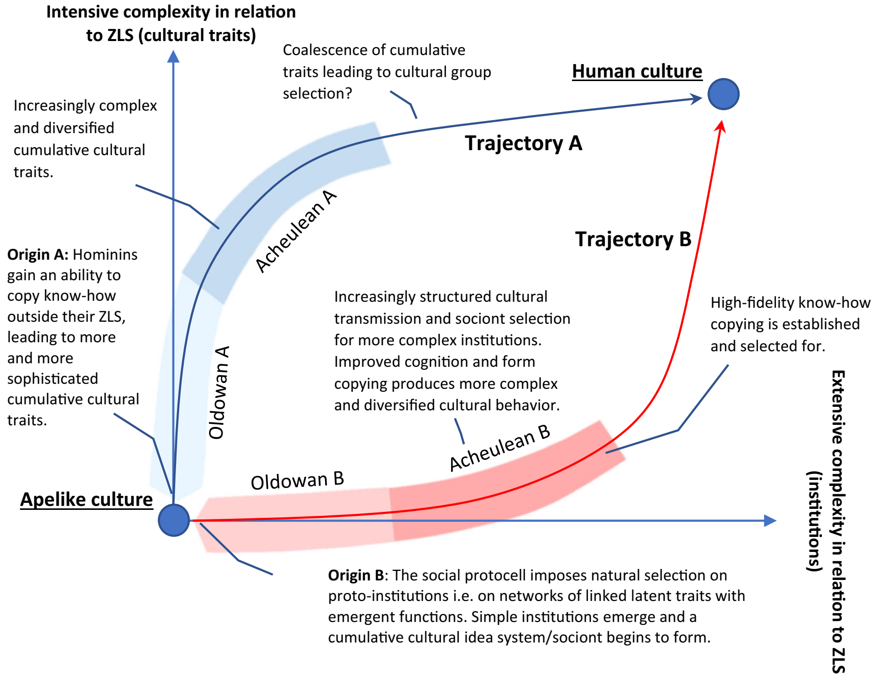


Fig. 7 Trajectories in the plane of cultural complexity. We here visualise cultural complexity on a plane, with extensive complexity (institutions) on the *x*-axis, and intensive complexity (cultural traits) on the *y*-axis. We place the starting point in the lower left corner, in an animal state where complexity, along both axes, is bounded by the creative capacity of the supporting species (its Zone of Latent Solutions). The end point is in the upper right corner which represents human culture, with high cumulative intensive *and* extensive complexity. We illustrate two possible trajectories **A**, **B** from start to finish, with the former representing the commonly imagined route, and the latter representing the alternative explanation proposed here. The figure also indicates different "versions" of familiar technological phases during human evolution, permitting us to ask which versions empirically seem to fit in better.

institutions targeting kill sites of large predators. In terms of sophistication and organisation, they were likely similar to chimpanzee nut-cracking.

Early hominin carnivory likely involved unmodified and locally available stone tools used for cracking large limb bones and skulls (left behind by scavengers) for marrow and brain (Pobiner, 2020; Thompson et al., 2019). As a proto-institution, such a strategy would be expandable by linking additional latent cultural traits into the existing network to add sub-functions, such as for finding carcasses, fending off competitors, performing more types of processing, provisioning suitable rocks, and so on. What we need to assume is that the hominins had some likelihood of linking latent traits together into persistent extensive networks, and that this ability could be evolutionarily improved over time (see *The adaptation of extensive culture*).

Large mammal carcasses have unusual properties that make them suitable for driving an ETI via the social protocell (see also Andersson and Törnberg, 2019, p. 91). First, this resource affords a ladder of increasing payoffs by earlier and better access to kill sites, whose lowest rung is plausibly accessible for an apelike ancestral hominin. Even if animal food was a minor part of the calory supply at this stage, it may still have been important as a source of bottlenecked nutrients (e.g., Pobiner, 2020; Tennie, et al., 2009). The following rungs would then be reasonably closely spaced and take the hominins from passive to more and more active and confrontational forms of scavenging, and finally to hunting (e.g., Bickerton and Szathmáry, 2011; Thompson et al., 2019). A second important feature is inherent to the size of the food parcels. Parcels that are too large to be consumed by single individuals invite coordinated and cooperative strategies since the cost of sharing is low (with “tolerated theft” as an entry-level mechanism; e.g., Blurton Jones, 1984; Winterhalder, 1996). The absence of similar features in the predominantly small and dispersed resources in the closed-canopy forest environment where *Pan* remained is then the proposed principal reason why the panine social protocell never triggered an ETI and open-ended cultural evolution (see e.g., Borg et al., 2022).

If some variants of carnivory institutions caused the communities that maintained them to grow and split more frequently than other variants (or communities lacking such institutions altogether), the social protocell could cause cultural group selection of an incipient sociont. We may truly speak of cumulative extensive culture at a point when communities were viable only if they supported socionts descended from parents with competitive variants of the carnivory institution.

The Oldowan may have begun to pop up when access to (more contested) fleshed carcasses came within the reach of variations of the carnivory institution. Access to soft tissue would present a motivation for inventing sharp stone tools since large parcels of soft tissue would be of limited value without them (e.g., Zink and Lieberman, 2016). But even if such tools may have been relatively easy to invent once the motivation was there (see *Oldowan know-how copying is less needed than widely assumed*), neither the tools nor the fleshed carcasses seem overly adaptive *alone*, which may point to an evolutionary coordination problem that is consistent with the observed slow and intermittent start of the Palaeolithic over its first million years (circa 3.0–2.0 Mya). Once both capacities did become firmly established and integrated together, their emergent fitness benefits would however come into its right. This may be consistent with the overall trend of Oldowan sites later on accelerating in frequency and geographic distribution (e.g., Plummer and Finestone, 2017).

The rise of the sociont as a group-level cultural unit of selection. The hominin carnivory niche went on to become the core of cultural specialisation in *Homo* (e.g., Stiner, 2002). The social protocell, however, would provide only a coincidental and pre-adapted degree of evolutionary individuality that cannot be expected to have carried far beyond the first steps up the evolutionary ladder of carnivory. To see how extensive cumulative culture could have expanded beyond its initial limitations, we must ask how the earliest sociont would have evolved to improve its evolutionary individuality during the hypothetical ETI. In practice this means accounting for how it internalised, extended, and adapted the basic evolutionary mechanisms provided by social protocell, to become better and better at responding as a unit to the selection pressures that acted on it; see *Becoming a cultural unit of selection*.

As discussed above (see *The selection of extensive culture*), latent cultural traits are weak units of selection and rather than seeking to suppress lower-level selection, it would be logical if the sociont improved its evolutionary individuality by expanding and shaping hominin *motivations* and *capabilities* for (i) copying latent cultural trait functions and (ii) via re-invention furnish the latent traits with know-how that was adequate for achieving the copied functions. Early on, such improvements may have followed as pure side-effects of expanding the primary function of the carnivory institution, since an increased cultural structuring of hominin behaviour itself may produce more and better opportunities for cultural transmission of any type (e.g., Nonaka et al., 2010).

There is no shortage of examples in the literature of adaptations that could further channel and adapt how *Homo* went about learning and expressing cultural traits, and that could have co-evolved with a stable extensive cumulative culture (such as in “human self-domestication”, see e.g., Hare, 2017, and the “cultural brain hypothesis”, see Muthukrishna et al., 2018). To take only a few examples, learning biases and improved assessments of the utility of cultural traits could facilitate linkage of cultural traits into networks (see *The selection of extensive culture*). Social tolerance, childhood, teaching, and pedagogy (e.g., Csibra and Gergely, 2011; Gärdenfors and Högberg 2017; Tehrani and Riede, 2008; Thompson and Nelson, 2016) could enable the maintenance of increasingly opaque latent cultural traits. Gesturing and proto-language would facilitate coordination and cooperation, and enable more types of cultural strategies to improve the specificity and flexibility in latent trait functions (e.g., Bickerton and Szathmáry, 2011). Later and more advanced adaptations could include language and norm systems to govern patterns of cultural transmission in high detail (Chudek and Henrich, 2011; Roughley and Bayertz, 2019). Finally, Griesemer and Shavit (2023) discuss evidence for processes for cultural group reproduction, such as by regulating transmission to achieve a complete set of cultural traits to offspring (which exemplifies potential adaptations to increase the fidelity of extensive cultural inheritance, see *The inheritance of extensive culture*), along with invention and innovation pathways (analogous to developmental processes) for producing adapted extensive cultural organisation from cultural knowledge (see also Davison et al., 2021, p. 228 including plasticity of cultural development).

The initially low risk of serious fitness conflicts between cultural traits and sociont could have increased when cumulative cultural traits appeared with a memetic potential for exploiting weaknesses in hominin psychology and cognition (see *The selection of extensive culture*). As a cultural unit of selection, however, the sociont would have access to such “memetic” tools of manipulation from the outset. Such exploitation may not have been easy to neutralise even when it conflicts with the fitness interests of the hominins individually. The exploited mechanisms would be there for *other* adaptive purposes, so avoiding the sociont’s attempts at “hacking” could easily have maladaptive net effects. The concept of "cognitive gadgets" (Birch and Heyes, 2021; Heyes, 2018, 2021) goes into detail about deeply embedded cultural brain structures that fundamentally modify our cognitive and psychological functions, and illustrates how the sociont may have had access to powerful and deeply seated pathways for imposing control over its hominin substrate.

Could not hominins have imposed *their* evolutionary will on the sociont? Even if hominins had the benefit of being strong units of selection all along, an increasing interdependence between *Homo* and sociont would seem to limit *Homo* more than the sociont in this regard. While hominins would typically depend on *one* sociont, the sociont would depend on *a community* of hominins. The difference is important since there would be many cases in which reducing the fitness of individual hominins could increases the fitness of the community as a whole (and thereby the sociont). Individual hominins could not blackmail socionts similarly. Unilateral exclusion would not hurt the sociont nearly as much, while the hominin itself would face forbidding risks and costs. Even if accepted into another community (which likely was *far* from certain), its social support network, family, and prestige would be lost, along with the value of all its knowledge that was specific to the original sociont and community. The sociont may thereby have had considerable options for using punishments and rewards to control the behaviour of hominins, and even breed them by culturally modifying their access to reproduction.

It is also well to note that while cheating and poor cooperation *between hominins* would limit the evolutionary design space of the sociont (by limiting extensive cultural states based on cooperation), *hominin* cooperation is still not a precondition for the sociont as such. It may initially have been based on merely coordinating hominin behaviours (again, the sociont arises from cultural traits, not hominins).

How extensive cumulativity could lead to intensive cumulativity. We will discuss two interacting ways in which an increasingly complex sociont could have produced pre-adaptations for adequate know-how copying by the time its presence has empirical support (circa 500 Kya, see *Oldowan know-how copying is less supported than widely assumed*). We argue first that *the need* would increase, and second that *the likelihood* of it arising would increase.

If extensive culture became increasingly complex, this entails that its constituent cultural traits would tend to become more and more specialised. Specialisation demands detail, however, so the reliance on re-invented know-how would more and more limit the further adaptation of the sociont. Since the primary benefit of know-how copying is that it permits more, subtler, and/or causally opaquer details in cultural know-how, it is fair to assume that it services would also be *increasingly needed* as a consequence of extensive cultural evolution along Trajectory B.

However, as long as the hominins lacked pre-adaptations for know-how copying (and other needed factors for cultural cumulativity) to appear in a minimally effective form (see also *Oldowan know-how copying is less supported than widely assumed*), the only remaining adaptive response would be selection on hominins for improved brain-based abilities to *invent* more detailed know-how. The implied brain enlargement would however become progressively more expensive, which is attested to by the battery of derived features that have enabled brain expansion in *Homo*, including for childbirth and post-natal brain growth, and high dependence of infants and mothers on social provision and protection (e.g., Dunsworth et al., 2012). The fact that brain enlargement still went so far in *Homo* also indicates that the selection pressures must have been crushingly strong.

By the time robust evidence of know-how copying in cultural transmission appears, the brain of *Homo* had since long gained a more modern layout (see e.g., Ponce de León et al., 2021) and even approached modern size and predicted performance (see e.g., Du and Wood, 2020; van Schaik et al., 2021). Apart from increases in inventive capacities, this may also have brought new and improved metacognitive capabilities, such as impulse and attention control, larger short-term working memory, theory of mind, and so on (see e.g., Dunstone and Caldwell, 2018; Heyes, 2016; Lombard and Gärdenfors 2021; Shea et al., 2014), which are centrally implicated in both invention and know-how copying in modern humans. This means that if extensive cumulativity drove the evolution of such capacities, their presence would also present an increasingly advanced pre-adaptation to make it more *likely* that *Homo* would gain an effective know-how copying capability (see Fig. 2). Trajectory B hereby provides increasing push *and* pull factors for the evolution of know-how copying.

Finally, to this brain-centred picture we should also add the recent attention that has been afforded to culture's own role in building sophisticated human brain function via "cognitive gadgets" (Ardila, 2018; Birch and Heyes, 2021; Heyes, 2018, 2021), including not least functions related to culture and know-how copying. Trajectory B tells us how a rich extensive-level system of cultural organisation may have appeared on top of existing brain capacities, not only shaping the further evolution of the brain, but also potentially pre-adapting us *culturally* for know-how copying, and many other abilities for utilising and maintaining culture in general (see also Tennie, 2018).

Trajectory A is in the scope of Trajectory B, but not the other way around. References to what we call extensive culture is ubiquitous in the prose and broader claims of research under Trajectory A (see Buskell et al., 2019). Still, Trajectory A says very little in detail about how intensive cultural cumulativity would actually end up giving rise to extensive cultural organisation (see Fig. 7).

The reason appears to be that extensive culture is outside of the zoomed-in analytical scope of Trajectory A. This leaves an analytical vacuum that has been an arena for debate as well as the introduction of a range of theoretical models and arguments to fill the empty space (e.g., Andersson et al., 2014; Fuentes, 2016; Griesemer and Wimsatt, 2007; Laland et al., 2000; Murray et al., 2021; Richerson et al., 2016; Smith et al., 2018; Zeder, 2018; Buskell et al., 2019). While strongly critical against ideas under what we call Trajectory A, these efforts do not critique its core account of the origin and early evolution of human culture as such, which means that these models and arguments still tend to conform to the overall logic and timeline of Trajectory A.

Reviewing these approaches is not in the scope of this article, but we will briefly comment on a family of Cultural Group Selection models and arguments in this vein (CGS, see e.g., Boyd & Richerson, 2010; Henrich, 2004a; Richerson et al., 2016; Smaldino, 2014; Soltis et al., 1995). Like Trajectory B, CGS *also* "zooms out" from the narrow focus of Trajectory A to propose that the culture of *Homo* has evolved on the group level. However, unlike Trajectory B, CGS does not challenge the overall logic and timeline of Trajectory A, which leads it to zoom out over *later* parts of human pre-history (primarily Upper Palaeolithic and later). Along Trajectory B, the sociont and *Homo* would at this point be firmly integrated by millions of years of mutualistic co-evolution, and it would be exceptionally hard to determine what the group-selected group *is really a group of*.

The nature of the units is indeed unclear, and CGS tacitly moves between and blends humans and cultural units in its analysis. This hinders the development of a detailed theoretical basis, and CGS focuses instead on arguing *that* cultural group selection has been at work. This question is less sensitive to the question of units, and CGS has indeed built a convincing argument in this area. Zooming out over a primordial context, Trajectory B begins from a much simpler and distinct set of units and interactions, which better supports a specific and sustained use of theory. This enables detailed hypotheses about how the original units and processes evolved downstream (not least by identifying the situation as a specific type of ETI) and reveals a potentially much more fundamental and earlier role for cultural group selection.

Discussion

Contradicting the self-evident. Social transmission of cultural traits is the lowest common denominator of culture in animals and humans, where the latter uniquely differs from the rest by incorporating highly derived mechanisms for faithful copying of know-how in a wide range of domains. Given that know-how copying is what ape cultural transmission most conspicuously lacks as an inheritance channel for cumulative evolution of know-how, what else could have been the roots of human culture than the appearance of know-how copying? What else could its earliest expressions be than Oldowan stone tools?

It is certainly no wonder that we have zoomed in so intently on this hypothesis. The problem is rather that without feasible alternatives it has *never fully served as a hypothesis*. While it has been explored in high detail, the aim has never really been to *test* it, but rather to furnish details to an apparently self-evident outline answer. This difference may be subtle, and the details that have been produced may, of course, also be used for testing it as a hypothesis (as we do here), but it is still an important difference since it affects how we react to anomalies. Not least since anomalies can almost always be plausibly put on the account of inherent empirical uncertainties. We argue, however, that if the anomalies that have emerged are taken seriously, and put together, they show that what has been uncovered is really a picture where Oldowan know-how copying seems increasingly less likely, less needed, and less supported by evidence.

We hold that the key reason why we cannot imagine feasible alternative origins from the perspective of Trajectory A is that it looks *too closely* at the circumstances where it seeks the roots of human culture. This is why we had to "zoom out" to discover Trajectory B as an alternative outline answer to that Big Question. Cultural traits and transmission remain of central importance under Trajectory B, but as one of *several* required parts of a larger machinery, namely the social protocell. Trajectory B tells us that the neglected extensive dimension of human culture may have been the first aspect of humanlikeness to evolve—not by transcending the Zone of Latent Solutions, but rather by expanding inside a surprisingly rich subspace of what apes and ape-like creatures can do without specialised know-how copying capabilities.

We argue that Trajectory B was *likely* because it does not rely on specialised abilities beyond expectations for an apelike early hominin, and that it was *needed* because it enabled a cumulative cultural pursuit of carnivory, which is the observed long-term ecological trend of our lineage over the past 3–4 My. We also argue that it may explain how know-how copying *became* likely and needed by the much later time when firmer evidence of know-how copying appears.

But is Trajectory B *supported*? Our critique of Trajectory A draws on a considerable body of research that has been produced under Trajectory A's own purview. Using this evidence to support Trajectory B requires careful (and admittedly complex) re-organisation, which we have only been able to foreshadow in selected contexts in this article and will ultimately require the production of new data under the purview of Trajectory B itself. Our aim has therefore been the more modest goal of arguing that Trajectory B is *sufficiently promising* to warrant further research to find out how it fares in more detail.

Data availability

Data sharing is not applicable to this research as no data were generated or analyzed.

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Notes

1. If behaviour is underpinned by *knowledge*, then "know-how" denotes knowledge about how to perform work to achieve specific effects (e.g., procedures to produce or use a tool, dance steps, etc.). Know-how is what we usually intend when we discuss "the stuff of culture", i.e., what it is that undergoes cumulative evolution. Other types of knowledge also play key roles in culture such as "know-where" (e.g., where the food is), "know-what" (e.g., what the food looks like), and so on (compare Buskell and Tennie, 2021, in press).
2. Candidate examples of cumulative culture in other species, including non-primates, have been put forward by several authors (see e.g., Whiten et al., 2021). To us, these examples primarily indicate a need for (and possibility of) sharpening the definition of cumulativity and further qualifying it with regard to what type of knowledge it applies to and in which domains (see also the endnotes in Tennie, Call, and Tomasello (2009) on this very point). For example, as we specify here, that it is cumulativity of *know-how* that revolutionised humanlike culture. Many cases put forward for cumulative culture in non-human species involve cumulative knowledge in other types and domains of knowledge (e.g., know-where, know-when, know-how in specific domains, etc.). Another qualification concerns the generativity of cumulativity. Human culture has been highly open-ended, which has not been the case in marginal and domain-specific cumulativity in other species, which thereby may not be analogous (e.g., bird and whale songs, see Fehér et al., 2009; Garland et al., 2022). Moreover, some of those cases (in particular in the vocal know-how domain) have come under recent attack (e.g., Mercado, 2022), and the dust has not yet settled on whether exceptional cases exist in other animals.
3. Actual know-how copying in apes is so simplistic that it barely qualifies as copying, such as social "triggering" of like behaviour (e.g., vocalisations, two-target tasks).
4. It is also relevant, for methodological reasons, to qualify the ability as a *spontaneous* ability, which is to caution for modified abilities in individuals that have been enculturated and/or trained by humans.
5. Within the ZLS, there can nevertheless be cumulative culture of other types of knowledge than know-how, such as know-where (generally labelled "step-wise traditions" by Tennie, Call, and Tomasello, 2009).
6. They have been reported to vary between, while being homogenous within, different regions (Read, 2012), which is at least consistent with a history as an evolved cultural feature. Moreover, variation in the effectiveness of this behaviour (with regard to its impact of the overall economy of the community) would likely produce swift and strong fitness effects on those variants (see e.g., Bowles, 2009; Zefferman and Mathew, 2015 for pertaining discussions about intergroup aggression and group-level selection).
7. One reason why this is an approximation is that many ETIs (e.g., multicellularity) are based on kin-selected cooperative groups, which is usually not referred to as group selection
8. Generally, apes are rather conservative, and even transfers between groups do not typically lead to the group adopting the traits of the transferred individual. If anything, the transferred individuals leave their traits behind and are socially induced to (re-)develop the locally shown mix of latent solutions (Luncz and Boesch, 2014, 2015; e.g., compare Luncz et al., 2012). This should not be confused with the much more complicated structure of modern human groups, where social units on this level of organisation are part of even larger units (e.g., Moffett, 2013). Strong social links may then exist on this level of organisation. Note that in contrast to chimpanzees, bonobo society is marked by much more laissez faire attitudes towards other groups. Encounters that would end in lots of violence in chimpanzees may end without problems in bonobos. But even in bonobos, most of the time, groups are apart and there is no confusion about who goes where.
9. If the component cultural traits are learned independently, the number of instances present in daughter communities after splitting should essentially be binomially distributed.
10. Two videos illustrating the dynamic are available at https://youtu.be/WLVa2Ae_vQM and https://youtu.be/GQu9ORywL7s.

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