Title

Did human culture emerge in a cultural Evolutionary Transition in Individuality?

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Abstract

The Social Protocell Hypothesis (SPH) proposes that the origin and evolution of human culture can be understood as an Evolutionary Transition in Individuality (ETI) and predicts that a "cultural organism" ("sociont") arose from a substrate of animal traditions contained in growing and dividing social communities. In the biological realm, ETIs have been responsible for the major transitions in levels of selection and individuality, and have given rise to the integrated hierarchical organization of life (e.g. the origins of prokaryotic and eukaryotic cells, multicellular organisms, and eusocial insects and primates). During an ETI, groups of individuals (here traditions) evolve into a new kind of individual (here the sociont). A central prediction of the SPH is that hominin cultural communities would have gained a threshold degree of individuality circa 2.5 Mya, triggering an ETI that drove the evolution of evolutionary individuality at the level of integrated traditions. We here assess the SPH by applying a battery of criteria – developed to assess evolutionary individuality in biological units – to cultural units across the evolutionary history of *Homo*. We find that *Homo* cultural communities increasingly meet these criteria, which buttresses the claim that they underwent an ETI in the cultural realm.

Keywords

Cultural evolution; Cultural Group Selection; Evolutionary Transitions in Individuality; Human evolution; Social Protocell; Sociont

Declarations

Funding: CA acknowledges funding by European Commission H2020 FETPROACT-2016 Action ODYCCEUS (Grant No. 732942).

Conflicts of interest/Competing interests: None.

Availability of data and material, Code availability, Ethics approval, Consent to participate, Consent for publication: n/a

Authors' contributions: See authors.

1. Introduction

Traditional behaviors are found in many animal species (Allen 2019; Galef and Laland 2005), but only in *Homo* have they coalesced into integrated and shared cultural systems (e.g. Andersson, Törnberg, and Törnberg 2014a; Read and Andersson 2019; Richerson et al. 2016; Smaldino 2014), and only *Homo* has come to specialize in maintaining and acting within such a system (e.g. via expanded cognitive and meta-cognitive functions; Csibra and Gergely 2011; Dunstone and Caldwell 2018; Shea et al. 2014; Sherwood and Gómez-Robles 2017; Sherwood, Subiaul, and Zawidzki 2008; Whiten and Erdal 2012). The integrated cultural nature of human behavior is strikingly expressed in emblematic feats of cooperation and coordination – such as when hunting like “a highly competitive group-level predator” (Whiten and Erdal 2012) – but it permeates the human way of life entirely and into its most minute details. For example, resources obtained using cultural hunting and foraging strategies go on to enter an intricate cultural “metabolic system” where they are processed, stored, distributed, disposed, and turned into a wide variety of products. These products themselves are part of the operation of this cultural system, which is much wider and older than its individual human stewards, who depend on it for their survival (e.g. Boyd and Richerson 2000; Henrich and McElreath 2003). This uniquely human “cultural community” embodies an emergent ecological strategy that cannot be reduced either to its learned or its genetic components, and that undergoes cumulative (or “ratcheted”; Haidle et al. 2015; Tennie, Call, and Tomasello 2009) evolution as a whole.

Tradition – Patterns of thinking and behavior (e.g. food preferences, foraging strategies, tools, social customs, etc.) that persists across generations due to social learning as young individuals observe older role models. Widespread among animals, traditions are foremostly adapted by creative problem solving, but with a potential for limited Darwinian selection arising from repeated cycles of learning and application.

Cultural component – Human cultural systems cannot generally be resolved into identifiable discrete traditions. To denote smaller parts of cultural systems more generally, we speak instead of cultural components. For particularly large and integrated cultural components we speak of **institutions**.

Culture – We reserve the term culture for integrated and adapted systems of cultural components (originally traditions.) Only the genus *Homo* supports culture in this view, and “an animal culture” is simply a collection of stand-alone traditions without significant interactions between them.

Social protocell – A system of independent features of social group behavior and learning that together creates (as a side-effect) a potential for sets of animal traditions to be selected together. Like the biological protocell – which plays a key role in the origin of cellular life – it imparts essential evolutionary functions (reproduction, heredity, and containment) to a potential future group-level evolutionary individual.

Cultural community – A social community of animals (in practice *Homo*) whose behaviors are largely governed by a cultural system that they enact, maintain, and transmit.

Sociont – The SPH proposes that groups of traditions evolved into a new kind of integrated cultural entity termed a sociont comprised of integrated cultural components. This is the evolution of evolutionary individuality that we investigate in this paper. The sociont is thereby a cultural community viewed as a cultural evolutionary individual rather than as a social group of hominins.

Evolutionary individual – An evolutionary individual is an integrated unit of selection and adaptation in which selection at lower levels is restricted. For instance, the multicellular organism is an individual as selection at the lower level of the cell is restricted.

Evolutionary Transition in Individuality (ETI) – Groups of individuals become a new kind of individual. In an ETI, formerly independent lower-level evolutionary individuals are integrated into a new group-level evolutionary individual. The lower-level entities cease, wholly or partly, to be evolutionary individuals in their own right – such as cells in a multicellular organism or organelles (e.g. mitochondria) in eukaryotic cells.

In many ways, this sounds more like the organization of an organism than an animal social community – except perhaps for some species of social insects, whose communities can be understood as an unusual type of organism due in part to the high degree of relatedness within colonies (Kennedy et al. 2017; Queller 2000; Queller and Strassmann 2009). For human cultural communities, however, these qualities cannot be understood genetically. While clearly underpinned by genetic adaptations, the exceptional range of behavior seen in human communities is not explained by genetic variation (e.g. Foley and Lahr 2011; Lewontin 1972). Our genetic adaptation in this regard is indirect – it *permits* cultural adaptation to happen.

So how could features seen as typical of (or even essential to) adapted biological organization appear from a substrate of social learning? In this paper we examine the Social Protocell Hypothesis (SPH; Andersson and Törnberg 2019), which proposes that this affinity between cultural and biological organization may be due to a deep similarity in how they originated and evolved. Our proposition is that a cultural unit termed a "sociont" evolved from collections of behavioral traditions as an Evolutionary Transition in Individuality (ETI; see Clarke 2014; Hanschen, Shelton, and Michod 2015; Leigh 2010; Maynard-Smith and Szathmáry 1995; Michod 1999, 2007; Szathmáry 2015).

ETIs are rare evolutionary transitions where new higher-level *evolutionary individuals* (entities equipped to undergo adaptation by natural selection as wholes; Buss 1987; Lewontin 1970; Sober and Wilson 1994) arise from cooperating groups of lower-level evolutionary individuals (Buss 1987; Hanschen et al. 2018; Michod and Roze 2001; Queller 2000; Szathmáry and Maynard-Smith 1995). Repeated ETIs have produced one of life's most familiar characteristics: its hierarchical structure. For example, groups of cooperative genes evolved into the first cellular genome, groups of bacteria-like cells evolved into the eukaryotic cell, groups of eukaryotic cells evolved into multicellular organisms, and groups of multicellular organisms evolved into social insect colonies.

Evolutionary individuality (Buss 1987; Michod 1999; Radzvilavicius and Blackstone 2018) emerges during an ETI via cycles of cooperation, conflict, and conflict mediation. Selection transitions to the level of the group, resulting in integrated and adapted entities whose lower-level units (originally evolutionary individuals) are co-opted and turned into parts of the whole. In this way, selection and adaptation transition from the lower level to the higher level of organization (Michod 1999). For a brief overview of ETI theory and its relation to frameworks such as Major Transitions in Evolution, see Hanschen et al. (2018).

The cultural ETI is proposed to have started with the emergence of hominin big game carnivory and the appearance of the genus *Homo* some 2.5 Mya. It is proposed to have been primed by a fortuitous combination of behavioral and ecological circumstances that imparted a basic level of evolutionary individuality (via community-level boundaries, heredity, and reproduction) to collections of unintegrated traditions present in growing and splitting early hominin social communities. The SPH thereby introduces a notable change of perspectives since "the group" is here a group of traditions, not of hominins.

The transition would have taken us from "animal culture" to human cultural communities – equipped with their own irreducible systems for heredity, reproduction, and development on the cultural group level, and with traditions becoming increasingly subordinated as component parts of the cultural whole. Following Andersson and Törnberg (2019), the hypothetical evolutionary individuals that emerged in this transition are referred to as *socionts* – cultural communities understood as units of selection in their own right. In this view, hominins are not seen as part of the emerging sociont but remain a separate genetic evolutionary individual, partnered with the emerging sociont in an unusual type of obligate mutualism between genetic and cultural evolutionary individuals. The nature of this relationship, and the evolution of *Homo*, is backgrounded in this paper, which is focused instead on the proposition that a cultural evolutionary individual, the sociont, emerged.

Arguably, the most fundamental question to pose about the SPH is whether – and, if so, when and to what degree – these cultural communities of *Homo* show evidence of having become evolutionary individuals; i.e. socionts. This question has many parts. For example, is there evidence that selection at an early point came to act collectively on lineages of animal-style traditions in early hominin social communities? Were integrated systems of traditions formed as a result? Is the function and organization of *Homo* culture consistent with what one would expect if selection increasingly acted on cultural communities as wholes? Is there evidence that these hypothetical cultural organisms (like biological counterparts) evolved mechanisms that increased the extent to which they could be targets of selection? These are the questions we seek to address in this paper.

We examine these issues by applying a set of criteria for assessing whether biological entities qualify as evolutionary individuals (Hanschen et al. 2018), adapting them to the cultural realm to account for the difference in substrate. We begin by outlining the SPH to explain why we think that an ETI drove human cultural evolution, and to introduce the entities used in the analysis. From this basis, we apply our criteria to judge whether, how, to what extent, and at roughly what stage, they are fulfilled. The analyses are then summarized and compared with selected types of biological evolutionary individuals, and the results are assessed and compared with theoretical expectations. We conclude by discussing the results and evolutionary individuality in the context of a set of features of human culture that appear to be inconsistent with our results.

2. From traditions to socionts via the social protocell: an overview

2.1 *Pan* as a proxy for early hominins

We use the traditions and community dynamics of *Pan* (in particular the more studied common chimpanzee *Pan troglodytes*) as a proxy for a primordial (pre-*Homo*) early hominin condition. Aware of the risk of conveniently over-stating similarities between *Pan* and early hominins (e.g. Sayers and Lovejoy 2008), our arguments rest in particular on assumed similarities in the following basic aspects of group behavior, social learning, and ecological strategy.

The diverse and broad range of traditions maintained by *Pan* include extractive foraging behaviors such as nut-cracking, leaf sponging, termite fishing, and ant-dipping, along with a wide variety of social conventions, food choices and so on (see Boesch 2012 for overview). These traditions are transmitted between individual apes primarily by copying outcomes (emulation) rather than underlying processes (imitation; Clay and Tennie 2018; Tennie et al. 2009; Tomasello 1996; Tomasello et al. 1987), and they may be stable and potentially long-lived (Mercader et al. 2007; Mercader, Panger, and Boesch 2002). Extant chimpanzees are believed to be qualitatively similar to the earliest hominins with regard to their capacity to form and maintain traditions (e.g. McGrew 2010; van Schaik 2016:78; Whiten, Horner, and Marshall-Pescini 2003), and it is likely that early hominins maintained traditions at a level and of a type similar to extant wild chimpanzees (e.g. Boesch and Tomasello 1998; Harmand et al. 2015; Lycett, Collard, and McGrew 2009; Whiten 2005; Whiten et al. 1999, 2003).

With regard to overall community organization, Pleistocene *Homo* appears to evolve from the basis of a *Pan*-like fission-fusion type of organization, through increasing refinement and the addition of new and intermediate levels of social organization (Grove et al., 2012; Layton et al., 2012) – not by shifting to some radically different type of group organization. Of particular interest is the community lifecycle of *Pan* (Andersson and Törnberg 2019:89; Moffett 2013:239–49). Communities arise and expire in irreversible, and roughly symmetric, fission events when social conflicts spiral out of control (Feldblum et al. 2018; Furuichi 1987; Goodall 1986). This becomes progressively more likely if group size increases and overburdens social cognitive mechanisms for handling conflicts and maintaining cohesion (Dunbar 1992, 1993, 1998). These rare events are under-researched but appear to be inherent to social features shared between *Pan* and *Homo*.

2.2 The social protocell

The centerpiece of the SPH is the so-called "social protocell" model, whose name derives from the protocell model of how early cells arose via an ETI in a substrate of primitive RNA molecules (Gánti 1975, 1997; Michod 1983; Norris and Raine 1998; Szathmáry and Maynard-Smith 1995). The claim is that the evolution of human cultural communities would have followed a similar pathway, but in a very different substrate. We will briefly review the argument by Andersson and Törnberg (2019).

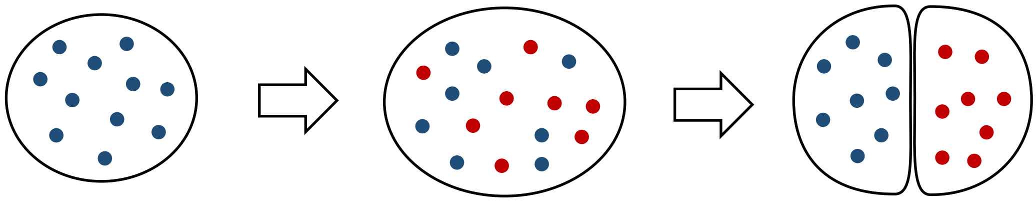

Figure 1 – The SPH proposes that social communities imposes a group-level lifecycle on collections of traditions, in the same way that protocells did with regard to proto-biotic RNA genes. Above, we compare idealized renditions of biological protocells with their proposed social counterparts to illustrate the parallelism.

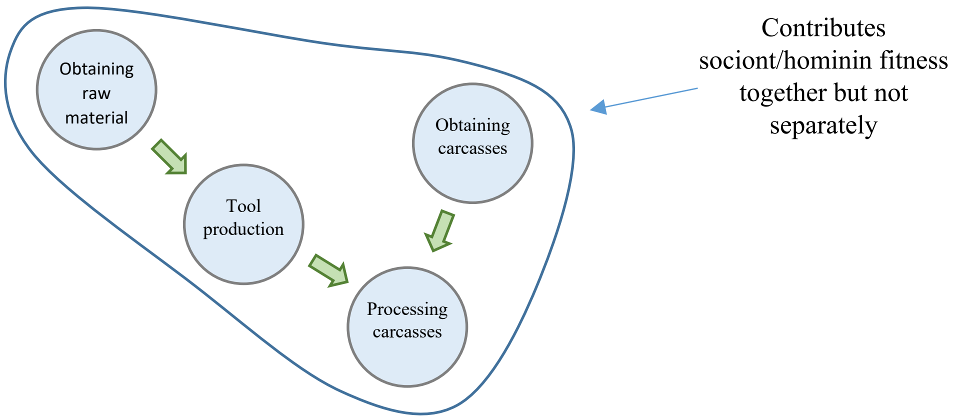

Figure 2 – Consider a minimal rendition of "the Oldowan carnivory institution." The components are behavioral traditions that occupy distinctly different regimes, in terms of time, location, type of behavior, and materials used. Many of these traditions are not functional on their own since they are adapted to be parts of a system that, in turn, produces something useful for the sociont (via the hominins) as a whole.

***Table 1**: Mechanisms behind primitive evolutionary individuality in biological and social protocells.*

Feature	Biological Protocell	Social Protocell	Meta-Evolutionary Function
Higher-level boundaries	RNA genes cannot pass through the lipid membrane vesicles generated as a by-product of their metabolism. They are thereby contained.	Traditions spread easily across tight social networks within social communities, but only rarely between communities since social links are absent or weak.	The boundaries concentrate and align the evolutionary fates of the contained units. This links their welfare partly to the welfare of their common container.
Higher-level reproduction	As the vesicle grows by internal addition of more lipid molecules, it destabilizes and splits into two daughter vesicles.	Communities tend to split roughly symmetrically at a rate that increases sharply as group size exceeds a critical threshold.	Reproduction is necessary for higher-level fitness as differences that develop between groups can now result in differential success in

Higher-level heredity	When the vesicle splits into two daughter vesicles (subject to assumptions about their size and symmetry) both vesicles will tend to contain the same mixes of RNA genes.	When communities split, the populations of both daughter communities are likely to carry similar mixes of tradition lineages, causing their overall traditional behavior to be similar.	Heredity enables natural selection on the higher level since features that affect the fitness of the containers may persist, vary and produce an evolutionary population.

The scenario begins in a set of circumstances that, as a side-effect, creates a potential for selection to act on groups of traditions contained in social communities (see Figure 1). This condition is claimed to be incompletely present in *Pan* communities today, and to thereby be likely to have existed also in early hominins (Andersson and Törnberg 2019:90–91; see also Section 2.1). The condition may be unpacked in terms of a system of three emergent evolutionary meta-functions – *boundaries*, *reproduction,* and *heredity* (Table 1) – on the group level. These functions potentiate the evolution of mutualistic *systems* of traditions.

Emergent systems of co-adapted traditions substantially expand the range of phenotypes achievable by social learning. Quite simply, you can do more (and different) things with a system of traditions than you can do with single traditions. We here refer to such adapted integrated systems of cultural components as *institutions* (see Richerson et al. 2016 for a discussion of institutions in a similar context). To illustrate, we outline "the Oldowan carnivory institution" in Figure 2 as a potential example of an early (ca. 2.6-1.8 Mya) institutional system of co-adapted activities, each in distinct domains and contexts, and each likely supported by separately transmitted traditional behavior (e.g. Roche, Blumenschine, and Shea 2009).[1]

Fitness on the level of the social protocell would be driven by the biological fitness contributed by traditions to the hominins maintaining them. If the hominins survived and reproduced at higher rates, so would the social protocell (Figure 1). But if traditions provided comparably small advantages, the fate of social protocells would be decided mostly by other factors, including the vagaries of chance. We therefore need reasons to infer that some important and widely available target, for which sophisticated institutional strategies would yield a substantial advantage, was available to early *Homo* but not to other early hominins (where, as in *Pan*, an ETI was never initiated.) Moreover, for evolution not to get stuck at an early point, this target must have kept yielding advantages as more and more sophisticated institutional strategies arose.

Cracking nuts or fishing for termites may provide adaptive additions to the diet, but they will hardly cause chimpanzee communities to decisively outcompete their neighbors. More generally, the rainforest resources available to *Pan* generally occur patchily and in small packages. Beyond a certain point of sophistication, the returns to increasing investments will thereby diminish. By contrast, *Homo* is uniquely associated with a resource that could have provided a strong and persistent competitive edge if pursued using cultural institutions, namely large game carnivory. The earliest stone tools (the Oldowan complex) would have been especially useful for processing carcasses, and large game carnivory went on to become highly developed and foundational to the lifestyle of *Homo* during the Pleistocene – across a widening variety of habitats and supported by sophisticated cultural systems (Bickerton and Szathmáry 2011; e.g. Gintis, van Schaik, and Boehm 2015; Stiner 2002; Whiten and Erdal 2012).

This provides a new way of envisioning the first steps in the transition from animal-style traditions to human culture via cultural group selection. The most consequential potential of the SPH is, however, that the fortuitous group-level meta-evolutionary functions of boundaries, reproduction and heredity (Table 1) *themselves* could be adaptively expanded and refined by the group selection that they enabled.

[1] Oldowan technology was variable but saw a progression from simpler to more sophisticated strategies with regard to for example long-distance transportation of raw material, raw material selection, tool production and hunting strategies. Our schematic illustration makes no claim to represent Oldowan culture as a whole or at any particular point in time or space.

That is what can be theoretically understood as *the evolution of evolutionary individuality,* and, as a consequence, the evolution of an integrated and adaptive group-level organization. The hypothetical outcome of such an evolutionary trajectory is what we refer to as a *sociont*: i.e. a cultural community as an integrated and adapted evolutionary individual.

3. Applying evolutionary individuality criteria to human culture

3.1 Background

A variety of criteria have been proposed by researchers to define and test whether candidate entities qualify as evolutionary individuals. In the following sections we will use the most commonly applied criteria as reviewed by Hanschen et al. (2017): *spatial boundaries*, *informational uniqueness*, *informational homogeneity*, *indivisibility*, *group level adaptations*, *division-of-labor*, and the applicability of a specific kind of multilevel selection termed *multi-level selection 2*. These criteria identify features that are generated by and/or enabling of group-level selection, and that are thereby likely to arise during an ETI, but unlikely to be seen otherwise (in particular together and in a highly developed state.) In this way we aim to test the SPH and systematically articulate the hypothesis in an empirical context.

For each criterion we first explain its role and importance with regard to evolutionary individuality. We then interpret these criteria in terms of cultural communities in *Homo.* We emphasize the Plio-Pleistocene origins of the social protocell, the early evolutionary history (primarily in the Oldowan), and finally we consider the trends across the evolution of *Homo* during the Pleistocene.

3.2 Spatial/temporal boundaries

3.2.1 Description

Boundaries constrain the components of lower-level units in ETIs, keeping them from diffusing between groups and from pursuing independent agendas that require free movement. During the origin of cellular life, the protocellular lipid membrane kept autocatalytic chemical networks (the lower-level units in that transition) contained inside self-replicating vesicles. Being stuck together in this manner facilitated the evolution of cooperation and eventually the integration of dispersed genetic information into a genome (Durand and Michod 2010; Jablonka and Szathmáry 1995; Maynard-Smith and Szathmáry 1995); see also “the boomerang effect” (e.g. Dugatkin 2002).

3.2.2 Analysis

In Section 2.2 we claimed that collections of traditions were stuck together within the social protocell. The boundary in this case is a lack of social bridges across which transmission can happen between communities (Table 1). The social protocell and sociont are thereby primarily bounded in a social rather than a physical space, although for *Pan*, and frequently (but not always) also for *Homo*, this social space corresponds to a physical space in the form of a territory.

Three factors that cause robust and persistent containment of traditions in *Pan* are:

1. Close and persistent social contact favors the transmission of traditions. Such contact is present within communities but rarely applies between communities (e.g., Boesch et al., 2008; Goodall, 1986; Schel et al., 2013; Wilson & Wrangham, 2003).
2. Enculturated individuals cannot transfer freely between communities (e.g., Nishida et al., 1979; Pusey, 1979; Wilson & Wrangham, 2003; Wrangham, 1979).
3. Enculturated individuals that do transfer are poor vectors of traditions, for example due to conformity bias (Haun et al., 2012; Luncz & Boesch, 2014, 2015; Van De Waal et al., 2010; Whiten et al., 2005) and rank bias (Horner et al. 2010; Kendal et al. 2015; Watson et al. 2017).

Although positive evidence is unavailable, it quite plausible that the factors listed above would have applied similarly to early hominins in a Pliocene primordial state. These are primitive examples of what

Durham (1992) labels Transmission Isolating Mechanisms, which were subsequently expanded and institutionalized during the evolution of *Homo*.

One reason to suspect that the containment of culture would have increased rather than decreased in *Homo* is that the more complex culture became, the more strongly its transmission must have relied on close and persistent social intimacy. On the level of social learning, cultural components tend to be opaque – indeed often both to role model and learner (e.g. Premo and Tostevin 2016; Tostevin 2007, 2019) – and their transmission relies on specialized and derived "pedagogical" adaptations (Csibra and Gergely 2009, 2011; Gärdenfors and Högberg 2017; Gergely and Csibra 2006; Kline 2015; Laland 2017; Tehrani and Riede 2008). On higher levels of organization, increasingly complex and integrated hominin institutions may have diffused less and less easily (Richerson et al. 2016:5): First, to be functional, all essential components of an institution must be effectively transmitted. Second, the institution, in turn, is integrated into some specific higher-order system of institutions, which means it will likely be much less adaptive elsewhere. Third, institutions, even more than focused skills, rely on liberal amounts of tacit knowledge whose function and even existence is unknown to the agents (Polanyi 1967).[2]

Direct empirical evidence of the timing and details are hard to come by, but interdisciplinary analysis suggests that the evolution of inter-community boundaries has a gradual and drawn-out evolutionary history across the Pleistocene (Grove et al. 2012). Layton et al. (2012) analyze data on the displacement of stone used for making artifacts (from Féblot-Augustins 1997) from the Oldowan to the Upper Paleolithic, in conjunction with estimated community sizes (Dunbar 1993; Hill and Dunbar 2003), and ethnographic as well as modeling analyses of area use. They conclude that movements of stone raw material remained mainly within small face-to-face coordinated social units (congruent with *Pan* communities) at least through the late Middle Paleolithic (until circa 50 kya, although simple inter-community institutions may have emerged locally before that; e.g. Blegen 2017; Brooks et al. 2018). Exchange of lithic material may be expected to follow networks of amicable social interactions, and the spread of lithic material should therefore overlap with the transmission of culture. In late Pleistocene and Holocene human societies, social boundaries are certainly under cultural control and exhibit complex specializations (e.g. cultural kinship, marriage, mythology, etc.; see e.g. Read 2012). Not least language (e.g. via dialects) is a powerful boundary mechanism, and its function as such may have been an important factor in its evolution; see (Moffett 2013:229–32).

Temporal boundaries are imposed by the irreversible community-level splitting dynamic, which the SPH views as analogous to cell division (see Figure 1). Social protocells, and later socionts, thereby have beginnings and ends.

3.2.3 Summary

Boundaries in a social space here play the role that physical boundaries play in biology, and although social spaces are frequently associated with physical territories, that is not always the case. These boundaries exist in *Pan* and thereby plausibly in early hominins, and they do not appear to have disappeared over time. To the contrary they seem to have become more and more effective as barriers to culture, institutionalized, and subject to cultural adaptation over time.

3.3 Informational uniqueness

3.3.1 Description

In the biological realm, informational uniqueness essentially means that each unit has its own independent genetic makeup. Units may therefore exhibit heritable individual differences, which promotes evolutionary individuality since it enables group-level variation that selection can act upon. In the SPH case, the heritable information is cultural rather than genetic, and we see cultural communities

[2] Polanyi (1967) describes how tacit knowledge – i.e. knowledge we are unaware that we possess – often prevents even simple acts of intentional transfer. Even between highly similar contexts (e.g. moving equipment from one factory plant to another), even if done systematically, with high motivation, and large resources committed.

as informationally unique to the extent that they possess their own independent and heritable sets of traditions or cultural components.

3.3.2 Analysis

Henrich (2004) describes and reviews evidence for four mechanisms that promote what we here call informational uniqueness; see also Boyd and Richerson (2010) and Chudek and Henrich (2011). These mechanisms suppress within-group variability and increase between-group variability in human behavior, assuming the presence of boundaries between groups. The first is *conformist* learning, which increases the rate of horizontal spread of favored traditions within a community and prevents established traditions from dropping out. The second is *prestige-biased* learning (Henrich and Gil-White 2001; Jiménez and Mesoudi 2019), which further increases between-group variation (e.g. Boyd and Richerson 1987) since it selectively disfavors ideas originating outside of the group, while it permits some internal sources of variation that can break up conformist lock-ins. The third is *punishment*; i.e. that the biological agents accept the cost of punishing non-conformers, which greatly amplifies the stabilizing effect of conformism (e.g. Boyd and Richerson 1992). Finally, *normative conformity* represents conformity for purely social reasons, regardless of whether the behavior in question is otherwise useful or not.

Conformism, *sensu lato,* is widespread among animals with social learning (de Waal 2013) and may contribute to maintain between-group variation in chimpanzees (Haun et al. 2012; van Leeuwen et al. 2012; Luncz and Boesch 2014, 2015; van de Waal et al. 2010; van de Waal, Borgeaud, and Whiten 2013; Whiten et al. 2005). However, it is a weaker force in *Pan* than it is in humans, who conform not only to gain access to better information, but also normatively in pursuit of social benefits (Haun, Rekers, and Tomasello 2014; e.g. Van Leeuwen et al. 2013). We thereby deem it likely that some form of conformism may have been present to a degree in early hominin communities and increased in *Homo* across the Pleistocene.

Chimpanzees may exhibit a bias towards learning from individuals with a high rank and/or a track record of success (Horner et al. 2010; Kendal et al. 2015; Watson et al. 2017). If present in early hominins, this may have worked as an innate evolutionary starting point for "prestige" as a derived and culturally institutionalized version, buttressed by genetic adaptations (Henrich and Gil-White 2001). The other mechanisms reviewed by Henrich (2004) are weak, different or absent in chimpanzees, and should consequently be viewed as derived during the evolution of *Homo*.

Some degree of informational uniqueness may thereby be theoretically expected in a primordial *Pan*-like state, and this is also supported by field studies. Substantial between-group variation in traditions has been found between chimpanzee communities (e.g. Boesch 2012; Kaufhold and Van Leeuwen 2019; Koops et al. 2015; Lycett et al. 2009; Sanz and Morgan 2007; Schöning et al. 2008; van de Waal 2018; Whiten et al. 1999, 2001). This indicates that collections of traditions in early hominin communities likely exhibited some degree of informational uniqueness.

We argued above that *Spatial/temporal boundaries* that constrained horizontal (between-group) transmission promoted informational uniqueness of groups, likely pre-dated, and then remained, throughout the evolution of *Homo*. Such boundaries to cultural dispersal, along with community-level heredity of *sets* of cultural components (Section 2.2; via community-level splits), and the factors promoting informational uniqueness described above, indicate that group cultures may have diverged over time due to selection or drift, rather than converging due to information flow.

Direct verification of cultural uniqueness in Pleistocene *Homo* is challenging to obtain. Evidence is poorly synthesized and a coherent picture is lacking (Kuhn 2020). Numerous individual studies, however, support an overall picture of ancient and persistent geographical cultural heterogeneity. Analysis of traces of butchering techniques at Bolomor Cave and Gran Dolina (Middle Pleistocene) shows evidence of persistent group-specific patterns that vary across time and space in ways that are not obviously functionally relevant (Blasco et al. 2013). Inter-community technological variation has also been inferred archaeologically in the earliest Oldowan (at Gona; see Stout et al. 2010, 2019), and Chinese stone tool industries between 300-40 ka yield evidence of persistent regional cultural distinctiveness, despite their apparent simplicity (Bar-Yosef and Wang 2012; Gao 2013). Foley and Lahr (2011) moreover suggest that cultural transmission by expansion of groups best explains observed patterns of geographic cultural variation over the past 100ky.

3.3.3 Summary

Taken together, informational uniqueness on the level of communities is present to some extent in *Pan*, and clearly present in more recent *Homo*. It is also indirectly suggested to have been present, and to have increased, during the evolution of *Homo*.

3.4 Informational homogeneity

3.4.1 Description

Informational homogeneity is maximized when all lower-level units in a biological individual carry the same genetic information. The fitness interests of the lower-level units are aligned by the fact (and to the extent) that it makes no evolutionary difference which unit reproduces (Hamilton 1964a, 1964b). Informational homogeneity thereby promotes group selection and provides an ideal setting for cooperation and so-called "fraternal" ETIs (Queller 1997) on the basis of kinship selection (e.g. Maynard-Smith and Szathmáry 1995; Michod 1999), such as when all cells in a clonally developing multicellular organism are genetically identical. In contrast, a low degree of homogeneity promotes competition and selection at the lower level, which can be problematic for the emergence of evolutionary individuality at the higher level.

3.4.2 Analysis

While informational homogeneity plays a central role in fraternal ETI, an evolutionary individual that arises via an "egalitarian" ETIs (Queller 1997; such as early cells arising from different species of RNA genes, or the eukaryotic cell arising from different species of bacteria) is *inherently* informationally heterogeneous. This fraternal type of ETI would also be the best match for the SPH since traditions and cultural components are clearly underpinned by different sets of information. The components of culture are thereby more analogous to diverse lineages of genes becoming integrated into a genome than they are to clonal cells becoming integrated into a multicellular organism.

In our case, the informational homogeneity criterion is therefore neither expected to be met from the outset, nor to emerge as an outcome of the ETI. But the criterion is still important since the analysis tells us that lower-level competition will remain a problem if the scope of group selection is to keep expanding via the evolution of evolutionary individuality. During an egalitarian ETI, conflicts are resolved by the evolution of conflict modifier mechanisms (Michod and Nedelcu 2003). We should expect to find examples of this type of mechanisms in a sociont, as we do in cells.

If competition between traditions in the emerging sociont is analogous to competition between genes in the emerging cell, then cellular mechanisms for managing and suppressing genetic conflict may offer guidance. The integration of independently replicating RNA replicator/interactors into a genome is arguably the most central evolutionary innovation in this regard (Maynard-Smith and Szathmáry 1993). The chromosome is a specialized monopolistic group-level replicator whose operation is based on, but not reducible to, the original lower-level replication mechanism of independent genes. It replicates its genetic units, and thereby the group-level genetic structure and proportions, in a centralized and controlled manner once every lifecycle (Ågren 2014; Durand and Michod 2010; Jablonka and Szathmáry 1995; Maynard-Smith and Szathmáry 1995). This produces a setting where parasitic genes are suppressed since they need to become part of the chromosome to gain access to replication.

The evolution of the chromosome may exhibit a suggestive parallelism with the highly structured and institutionalized enculturation process that emerged in *Homo* (e.g. Read and Andersson 2019:2–3); see also the discussion of related processes by Smaldino (2014:250–51). A normative canon of cultural knowledge is here transmitted in a structured and cumulative sequence, following a modified and expanded process of physiological development, using adaptations for cultural transmission (Section 3.2.2), that are unique to *Homo* (e.g. Han and Ma 2015; Thompson and Nelson 2011, 2016). Such an integration and monopolization of cultural heredity would stabilize higher-level cultural organization and make it more heritable, but it would also cause parasitic cultural elements to be less likely to spread and disrupt the function of a sociont. The ability of cultural components to reproduce would become tied to admission into such a canon, which may require, for example, fitting functionally and logically into the prevailing system of customs and skills, and, not least, being considered part of the norm (see e.g. contributions in Roughley and Bayertz 2019). Without such a normative centralized system, new traditions could suddenly arise to exploit some feature of the sociont or the hominins (cognitively or psychologically) to spread and disrupt the integrated function of the sociont.

3.4.3 Summary

The sociont does not exhibit informational homogeneity, and it is not predicted by the SPH to do so. Provisionally an example of an egalitarian ETI, it should be expected to instead exhibit derived adaptations for suppressing lower-level competition between cultural components.

3.5 Indivisibility

3.5.1 Description

Indivisibility means that one cannot separate the parts out from the whole and maintain thes functional properties of the whole. This increases the likelihood that selection will act on the integrated unit than on separate parts. It is therefore indicative of evolutionary individuality if separated subunits do not maintain properties of the whole and cannot survive on their own outside the group context (Michod 1999, 2007).

One mechanism by which indivisibility can emerge is when components specialize and lose vital features that are taken over by other specialized parts; see also Section 3.7 below. For example, cells in differentiated multicellular organisms have specialized in varied internal functions in the organism and lost the ability to reproduce and survive independently in this process. The same fate has befallen bacterial mitochondria and plastid endosymbionts of eukaryotic cells, and, likewise, the specialized castes of social insects. Once this has happened, the fitness of one component is dependent upon other components of the group. Indivisibility indicates a low level of conflict between lower-level units since the dependencies that make the individual indivisible act to align fitness interests on the lower level.

3.5.2 Analysis

Since the sociont is composed of interacting cultural components, indivisibility means that components on any level of organization are unlikely to function well outside of the group context; see also Section 3.3, where some problems pertaining to inter-community transmission of cultural sub-units were discussed. As a limit case, we may readily establish that institutions in modern-day human societies make little sense on their own. We could not take the institutions of a society and create functioning societies each using subsets of the parts – banking in one, police in the other, daycare in the first, and so on. There has to be a relatively full set of complementary functional units in place. This logic permeates the entire internal hierarchy. Dividing institutional units on any level in this way incurs exactly the same set of problems, and the principle is particularly clearly expressed in technological systems, which are eminently indivisible.

This form of indivisibility is inherent to modular adapted systems, which we have argued may have emerged early (circa 2.6-1.8 Mya); see the "Oldowan Carnivory Institution" (Section 2.2. and Figure 2). By contrast, sets of traditions contained in *Pan* communities are divisible. Removing or adding one traditional practice – such as nut cracking or ant dipping – is unlikely to affect the function or transmission of other traditions since they lack interdependencies. The same would be true for a collection of early RNA species compartmentalized by a lipid membrane boundary. The traditions contained in the early social protocell (or present-day *Pan*), just like the genes in the early biological protocell, are divisible *in principle*. However, due to the protocellular dynamics (see Figure 1 and Table 1) they would still not be divided regularly *in practice*. They would typically remain together, which would favor the evolution of dependencies, and thereby *actual* indivisibility.

3.5.3 Summary

Sets of animal tradition lineages contained in the social protocell are divisible in principle but rarely divided in practice. Actual indivisibility would then have arisen during the evolution of the sociont, with the sociont being increasingly indivisible the more complex its institutional organization became.

3.6 Group-level adaptations

3.6.1 Description

Group-level adaptations provide evidence of group selection but identifying them can be challenging. Groups can have features that look like group-level adaptations but that really are properties driven by selection on the lower-level that filter up to the level of a group (Shelton and Michod 2014, 2020). Williams (1966) illustrated this by way of describing how a "fleet herd of deer" is really just a “herd of fleet deer” where the group-level property may be described as a "fortuitous benefit" (Williams 1966) or a "cross-level byproduct" (Okasha 2006) of lower level properties.

Key to telling true group-level adaptations from cross-level byproducts is to determine whether fitness has truly been “exported” from the lower level to the group level, or if the fitness of the group is simply an aggregative property of lower-level traits (Michod 2007; Michod and Herron 2006). In other words, have the lower-level units sacrificed their fitness as independent individuals in return for a greater contribution of fitness via the higher level? We may subject claims of group-level adaptations to a test by asking whether carrying the trait would cause the lower-level entities to suffer a reduction of fitness if they left the context of the group. Being fleet, for example, fails this test since being fleet would not be detrimental to a deer if it left the group.

3.6.2 Analysis

Do the components of cultural systems have properties that would cause them to have lower fitness if they left their cultural context? Are such properties linked to adaptive properties of the cultural system that they benefit from being part of? If so, we may be looking at traits selected on the group level.

Richerson *et al.* (2016) conclude that institutions are group-level features; see also Smaldino (2014) Although their analysis is mostly set in relatively recent times, we think a similar argument can be made from very early on. If we pose the question formulated above about the Oldowan carnivory institution (Figure 2), we find that its constituent components will certainly suffer if moved to another setting, and that they will do so *because of* how they are adapted to serve their roles in the institution as an integrated whole. For example, making stone tools without the knowledge of how to obtain animal carcasses would be minimally beneficial and perhaps maladaptive. This contrasts with animal traditions (such as nut cracking or termite fishing among chimpanzees) which would seem to be equally adaptive regardless of the context of other traditions.[3] Institutions then become more and more prevalent and complex the closer we get to modern times.

3.6.3 Summary

Group-level adaptations are absent (or marginal and not so far detected) in *Pan* communities. They seem to have arisen early – and to have increased in complexity, integration and importance – during the evolution of *Homo.* Institutions such as large game hunting may be group-level traits.

[3] It should be noted that group-level features in primates is an under-researched topic and that it cannot be ruled out that marginal examples would exist (van de Waal 2018).

3.7 Evolutionary Division of Labor

3.7.1 Description

To avoid confusion, let us first state that division of labor in anthropology (and in social science generally) refers specifically to the division of tasks and specializations between human individuals (e.g. Kuhn and Stiner 2006). Evolutionary theory uses a more general understanding of division of labor as a division of tasks and specializations between any types of components. For example, differentiated multicellular organisms exhibit division of labor between specialized cell types, cells exhibit division of labor between organelles, and social insect colonies exhibit division of labor between castes. When some component parts specialize on survival while others specialize on reproduction, the term "reproductive division of labor" is typically invoked. Since cultural components rather than hominins form the parts of the sociont, we here refer to division of labor as occurring between cultural components.

Evidence of division of labor in an entity is evidence of "near-decomposability" – a universal principle of organization and design (see e.g. Andersson and Törnberg 2018:129–31; Marengo and Dosi 2005; Querbes, Vaesen, and Houkes 2014; Simon 1962; Wimsatt 1975). Specialized functions have been broken down into complementary sub-functions and organized into systems, frequently in several hierarchical levels, to thereby greatly simplify and structure the internal organization. This modular organization is evident in all but the very simplest adapted entities, and it is widely seen as a precondition for evolution or design of complex adapted organization. Division of labor is thereby evidence that fitness has been exported to the level of the group, and that the new higher-level entity is now the evolutionary individual.

3.7.2 Analysis

Under the criteria of *Indivisibility* and *Group-level adaptations* we have already described several examples of institutions that clearly exhibit this form of division of labor. For example, the components of the "Oldowan carnivory institution" are specialized in delimited sub-tasks and make sense only together with the other co-adapted components (see Figure 2). Archaeology robustly reveals a trend toward deepening cultural division of labor, both as observed in the products of culture (e.g. complex technology; see Haidle et al. 2015), and in what we refer to as institutions; see also Smaldino (2014). This trend of diversification and increasing narrowness of specialization has continued and accelerated into the present (e.g. Beinhocker 2006).

This qualitatively differentiates *Homo* from other animals, including *Pan*. The traditions maintained by chimpanzees exhibit diversification but *not* integration of function beyond what can be achieved cognitively in creative problem solving (within the "zone of latent solutions"; e.g. Reindl, Bandini, and Tennie 2018; Tennie et al. 2009). We take this to imply that pre-Oldowan hominin traditional repertoires (like *Pan*) likely did not exhibit division of labor.

3.7.3 Summary

Our observations lead us to conclude that cultural evolutionary division of labor arose and deepened during the evolution of *Homo*, and that it is not evident in other species maintaining traditions, including *Pan*.

3.8 Multi-Level Selection 2

3.8.1 Description

Damuth and Heisler (1988) seminally described a subdivision in the debate about multi-level selection in terms of two types of models: Multi-Level Selection 1 (MLS1) and Multi-Level Selection 2 (MLS2.) They characterized these as follows ("individual" here corresponds to our use of the term "lower-level"):

The criteria for MLS1 are as follows:

1. "Group selection" refers to the effects of group membership on individual fitness.

2. Fitnesses are properties of individuals and group fitness is an aggregative property of individual fitnesses.
3. Characters are values attributed to individuals (including both individual and contextual characters - see below).
4. Populations consist of individuals, organized into groups.
5. Explicit inferences can be made only about the changing proportions of different kinds of individuals in the whole population (the meta- population).

The criteria for MLS2 are as follows:

1. "Group selection" refers to change in the frequencies of different kinds of groups.
2. Fitnesses are properties of groups.
3. Characters are values attributed to groups (including both aggregate and global characters).
4. Populations consist of groups, composed of individuals.
5. Explicit inferences can be made only about the changing proportions of different kinds of groups in the population.

In essence, when MLS2 models are applicable, that means that we are dealing with groups that have become evolutionary individuals. MLS1 models capture situations where the entities do not constitute proper parts of a group-level individual and where we cannot yet speak of group-level adaptations. Okasha (2007) furthermore remarked that there is a characteristic temporal ordering where MLS1 may turn into MLS2, so we may have both types of dynamics in place at the same time.

3.8.2 Analysis

The ETI proposed by the SPH begins from an MLS1 scenario in which traditions initially are not integrated as parts of a higher-level system. They simply happen to be organized into groups of traditions as a by-effect of early hominin group behavior, which maintains persistent social groups of hominins, with the coincidental effect that they contain lineages of traditions (see Section 2.2). Initially, the fitness of such a group of traditions is an aggregative outcome of the traditions within that social community. Interactions between traditions are minimal and likely not synergistic. As a result of these minimal interactions, characters and fitnesses may be assigned to individual traditions[4] but not to groups of traditions, except in the aggregate sense.

While the community structure of *Pan* causes traditions to be organized into groups, the traditions themselves exhibit differential fitness and may be marginal units of selection. The frequency of any given tradition can be examined across chimpanzee communities, though traditions may be bounded within communities due to chimpanzee behavior and social structure (Luncz and Boesch 2014, Van Leeuwen et al. 2014). Chimpanzee traditions can be transmitted between chimpanzees and spread within social groups. These traditions are often group-specific and spread when chimpanzees observe conspecifics performing the behavior. Not all traditions are acquired by every member of a social group; the presence of transmission with some degree of fidelity and differences in the frequency of traditions sets the stage for selection to act on traditions.

As the ETI progresses, simple institutions appear, such as “the Oldowan carnivory institution” (Figure 2), where traditions become functional units of larger systems. The adaptive functions (such as contributing meat or other resources) of such institutional groups of traditions in *Homo* are emergent, as they are determined by complex, nonlinear interactions between traditions. We may thereby speak increasingly of fitness on the cultural group level rather than on the cultural component levels, and we are also more and more inclined to speak also of properties of these systems as wholes. Since traditions

[4] We here need to keep track of the difference and linkages between (i) the biological fitness contribution that a traditional strategy may have to its carrier, and (ii) the fitness of the tradition itself in terms of its likelihood of spreading between carriers.

interact and co-occur, changes in sets of traditions (and more generally cultural components) across space and time can be characterized. The sociont is therefore consistent with a MLS2 framework.

3.8.3 Summary

The observations that we have made in prior sections support an interpretation where an MLS1 situation gradually turns into an MLS2 situation during the evolution of *Homo.*

4. Results

In Table 2 we summarize our findings along with biological examples for comparison. The **Eukaryotic cell** (like the sociont) stems from an egalitarian ETI (eukaryogenesis) and is also the starting point of a fraternal ETI: the evolution of **multicellular organisms**. **Colonial organisms that develop clonally** (e.g. the volvocine green algae Eudorina elegans) represents an intermediate stage in this transition. The **Pan/early hominin social protocell** is a pre-ETI starting point exhibiting only pre-adapted evolutionary individuality. **Early Homo** represents the social protocell once it is undergoing an ETI. **Homo** represents the sociont, which is the proposed result of the cultural ETI: an integrated cultural unit that fulfills most of the individuality criteria.

For each applied criterion there is also a theoretical expectation that may be argued from the standpoint of the evolutionary trajectory that is invoked. For an egalitarian ETI beginning from “a protocellular situation”, we may predict as follows:

At the social protocell stage, **informational uniqueness should be fulfilled** at least to some extent since this is necessary for selectable variation (this is also referred to as “between-group variation”). Social protocells are also expected to **not be informationally homogenous.** Many types of lower-level entities co-exist stably within them as they do not compete directly (e.g. traditions aimed at different foraging tasks). A social protocell **is divisible** in the sense that the fitnesses of lower-level entities do not depend on the presence of other types of such entities. Although internally heterogenous, the lower-level entities (individual traditions) are not initially organized into systems and exhibit **neither division of labor nor group-level adaptations** at the outset. On the same account, protocells **do not exhibit MLS 2**. The protocell is by definition expected to exhibit **temporal and spatial boundaries**.

Beyond the protocell, an ETI should lead to all these criteria to be fulfilled to an increasing degree as a result of selection for evolutionary individuality. **The exception is informational homogeneity**, whose functional effects will be achieved by the evolution of other conflict modifiers. The multicellular organism – our example of a fraternal ETI (Table 2) should, on the other hand, be expected to also exhibit informational homogeneity (see *Informational homogeneity*).

We find that our assessments match up with theoretical expectations, as well as with the biological examples that we used for comparison. Our findings are consistent with the SPH hypothesis that a cultural evolutionary individual emerged as the outcome of an ETI that may be described as egalitarian.

***Table 2**: Comparative summary of the application of criteria for evolutionary individuality.*

	Eukaryotic cell	Colonial organism that develops clonally	Multicellular organism	*Pan*/early hominin – social protocell not undergoing an ETI	Early *Homo* – social protocell undergoing an ETI	*Homo* – proposed sociont organism
Spatial/temporal boundaries *(Section 3.2)*	**Yes**. The cell is a cohesive whole and arises in a fission event. It dies in fission or by other causes.	**Sometimes.** If the cells can leave the group and reproduce on their own, then spatial boundaries are absent.	**Yes**. The organism is a cohesive whole, with spatial boundaries, birth, and death.	**Yes**. Territorial behavior ties social networks to a spatial boundary. Like cells, communities arise and die in community fission events, and if they fare poorly in competition.	**Yes**, see *Pan*. Notably the primary boundary is in a social rather than geographical space. The social boundary may or may not correspond well to the defense of non-overlapping territories.	**Yes**, see *Pan*/*Early Homo*. Boundaries gain internal structure, and their cultural control today must reasonably have emerged across the Pleistocene, although details and timing is hard to determine.
Informational uniqueness *(Section 3.3)*	**Yes**. If reproducing sexually.	**Yes.** If reproducing sexually.	**Yes**. If reproducing sexually.	**Yes**. Group boundaries prevent horizontal information spread, thereby preventing uniformity in group composition. Degree of informational uniqueness depends on how cultural information is distributed among daughter colonies when communities split.	**Yes**, see *Pan.* Informational uniqueness is further promoted by the emergence of early institutions, which hampers the lateral transfer of traditions.	**Yes**, see *Pan* and early *Homo.* Informational uniqueness may have increased over time as institutions became more complex.
Informational homogeneity *(Section 3.4)*	**No**. Egalitarian ETIs do not exhibit informational homogeneity. The genomes contained within the eukaryotic cell contain different information.	**Yes.** Since development is clonal, all cells are genetically identical and arise from a unicellular stage. Informational homogeneity is an outcome of a fraternal ETI.	**Yes**. Since development is clonal, all cells are genetically identical and arise from a unicellular stage. Informational homogeneity is an outcome of a fraternal ETI.	**No**. Different traditions are not underpinned by the same information.	**No**. Egalitarian ETIs do not exhibit informational homogeneity. The traditions contained within the sociont are underpinned by different information.	**No**. See *Early Homo*.
Indivisibility *(Section 3.5)*	**Yes**. The components of a eukaryotic cell are part of an integrated cellular system.	**Sometimes.** In some species, cells can leave the group and reproduce on their own; for other species, the colony stays together throughout development.	**Yes**. Due to the single-cellular state and specialized reproductive cells, the cellular level is indivisible. On higher levels parts (tissue, organ, etc.) are	**No**. The collection of traditions contained within a community may be divided since they are not co-dependent.	**Sometimes.** The incipient sociont organization of the social protocell is **increasingly indivisible**. Dependencies between traditions may arise, resulting in the evolution of institutions.	**Yes**. The system of cultural components is a functionally integrated whole. Components are not viable on their own and their contribution to fitness (cultural and biological) depends on

			functionally integrated and lack separate fitness.			their co-adapted cultural context. Fitness has been exported to the new higher level of selection.
Group-level adaptations *(Section 3.6)*	**Yes.** Eukaryotic cells have numerous adaptations, including membrane-bound organelles and meiotic reproduction.	**Yes.** Generally including cell number control, with the specific adaptations dependent upon the species in question.	**Yes, and increasing relative to undifferentiated ancestors.** These include cellular differentiation, tissue specialization, etc., with specific adaptations depending on species.	**No, or marginally**. While under-researched in primates, animal traditions do not appear to possess emergent properties that arise from their interactions.	**Increasingly from initial low level**. The integration and differentiation of institutions, originally around carnivory, likely driven by selection on the cultural system as a whole.	**Yes**. Human culture is highly integrated and institutions appear to be group-level adaptations.
Evolutionary division of labor *(Section 3.7)*	**Yes**. An integrated cellular system consists of complementary and specialized intracellular components.	**No.** Cells are undifferentiated and unspecialized.	**Yes**. Cells are differentiated into cell types with different functions and differential expression of a uniform informational underpinning.	**No**. Traditions have different domains but are not integrated, so there is no higher-level labor to divide. Internal division of labor between components of traditions is explainable by cognitive processes.	**Increasingly from initial low level**. Integrated and internally organized institutions should emerge at the outset of ETI and this appears to have happened early in the evolution of *Homo*.	**Yes**. An integrated cultural system consists of complementary and specialized cultural components, e.g. in domains like mobility, tool production, hunting, sharing, comfort, etc.
Multi-level selection 2 *(Section 3.8)*	**Yes**. Eukaryotic cells have emergent properties, are integrates, and form lineages in which both genomes survive and reproduce as a whole.	**Sometimes.** Depending on the organism's traits (e.g. presence of obligate coloniality, emergent or aggregative survival and reproduction), MLS1 or MLS2 may apply.	**Yes**. Early-onset group selection by close kinship between clonally reproducing protists.	**No, or very weakly**. Selection still takes place primarily on the level of traditions, and lineages consisting of integrated units of traditions are absent (or at least marginal and undetected so far).	**Increasingly**. Carnivory provides a target around which increasingly sophisticated and integrated cultural systems can form. These cultural systems have emergent properties and can give rise to lineages of systems.	**Yes**. The fate of higher-level entities (integrated cultural systems) is of primary interest: cultural systems have emergent properties and survive and reproduce as a whole.

5. Discussion

We tested the SPH by subjecting it to a range of criteria previously developed to identify evolutionary individuals. Many of these criteria correspond to mechanisms that promote selection at higher levels (Hanschen et al. 2017, Clarke 2013). We examined *Pan* as a proxy for early hominin cultural groups, evidence of culture in early *Homo,* and later for *Homo* cultural groups. We found that later *Homo* cultural groups satisfied more individuality criteria than did early *Homo,* and that early *Homo* cultural groups in turn satisfied more individuality criteria than did *Pan.*

Taken together, our analyses indicate that the degree of evolutionary individuality of cultural communities increased during the evolution of *Homo*, which, in the context of the SPH, points to deep-seated similarities between the evolutionary provenances of human culture and biological organisms. But the idea that human culture has more than superficial similarities with biological organisms is clearly controversial in biology as well as social science (see e.g. Dunn 2016:11–31 for a review). We will therefore end by discussing the evolutionary individuality of cultural communities in the context of four salient differences between human culture and biological organisms.

Let us first briefly remark on what sort of similarities and differences the SPH should lead us to expect. The SPH implies that human cultural communities and biological organisms represent outcomes of the same type of evolutionary process – an ETI – operating on two different substrates, namely genetic variation and cultural variation (i.e. in the spirit of "general" or "universal" evolutionary theory; see e.g. Aldrich et al. 2008; Andersson 2008; Campbell 1974; Cziko 1995; Dawkins 1983, 1992; Hull 1980). The expectation is thereby that differences in outcome are attributable to differences in substrate (socially learned behavior vs. biochemistry) rather than to fundamental differences in the evolutionary process.

5.1 First difference: are cultural communities more like an ecosystem?

Recent societies are more often likened with ecosystems than with organisms. Components (e.g. institutions, technologies, firms, persons, etc.) may gain, lose or not be affected by their interactions, and analogues of all types of ecological interactions are represented (in addition to cooperation also competition, neutralism, parasitism, commensalism and amensalism; see e.g. Sandén and Hillman 2011). In other words, ecological interactions are not primarily cooperative (Ings et al. 2009), unlike the interactions between parts of evolutionary individuals (Michod 1999). Ecosystems are not units of selection (Huneman 2014) and they lack characteristics that would cause them to fulfill the individuality criteria discussed above. This raises the question as to whether the SPH overstates the similarity between cultural communities and biological organisms.

The time frame of the sociont (and of this study) is important in this context. The SPH places the base of the ETI at circa 2.5 Mya (see Section 2.1), at which time (and before) face-to-face coordinated social communities, strongly bounded upward in size by cognitive capacity (e.g. Dunbar 1993; Hill and Dunbar 2003) were, and then appear to have remained, the top level of social and cultural organization, until some 50 – 100 kya (e.g. Moffett 2013, 2019). Larger and more aggregated social units then arose and became dominant during the Late Pleistocene (see *Spatial/Temporal boundaries*). During the Holocene, cultural and social organization kept expanding dramatically in level upon level. The sociont coincides with ancestral cultural communities of the older and smaller style.

These more recent and larger aggregates would have required institutions extending between and above the level of the sociont to handle inter-community conflicts (Gat 2010; Wilson 2013). Embedded in such institutions, the sociont unit itself would have to adapt to new and changed roles in a new, larger system. The new aggregated units would also be much larger, and there would be fewer of them, which would inhibit group selection on levels above that of the sociont (Traulsen and Nowak 2006). If anything, selection on cultural groups would thereby have waned in importance in an increasingly fluid multi-level organization, with less institutional checks on non-cooperative interactions (Andersson and Törnberg 2018; a "wicked" system; see Andersson, Törnberg, and Törnberg 2014b).

There is no reason to think that these more recent higher- and multi-level societies would be organized in the same way as the sociont components that they once emerged from, although future work is needed to confirm this. The suitability of ecological models to recent society thereby does not contradict the suitability of an organismal model for ancient societies. The first difference thereby primarily stands out on a comparison between *recent* human societies and biological individuals.

5.2 Second difference: internally generated adaptive traits

While adaptation in biology mainly operates on randomly generated changes in genes and genotypes, adaptive traits in cultural communities (including heritable features) frequently arise by internal innovation. Hominin creativity, and trial-and-error on a fine level of resolution, reacts much more rapidly than selection could have worked on variation on the sociont level. This internal and goal-directed nature of some cultural change raises the question: To what extent do we need cultural group selection to explain cultural adaptation?

Let us look at cultural evolution in action in more detail. High-resolution examples are hard to find in the deep past, so we will consider how a major institution arose across the interface between the late Epi-Paleolithic and the earliest Neolithic. Stiner *et al.* (2018; 2014) have described in detail how goat domestication arose over the course of more than a millennium at Aşıklı Höyük (AH; Central Anatolia) – going from advanced herd management strategies for wild populations, to fully domesticated animals penned and managed within the settlement (see also Abell et al. 2019). What Stiner and colleagues describe is a multi-generational process where novel solutions, in an iterative and cascading manner, produce new problems to solve and opportunities to pursue. For example, penning goats within the settlement reduces losses to predators, but creates additional problems, such as with pests. These cascades of change propagate through society as a whole, leading in the end not only to a new institution, but to the integration of this institution as a functional component of the internal organization of the cultural community.

Several generalizable observations can be made in this example. First, humans here engage collectively in a dynamical and creative innovation process where solving problems and pursuing opportunities generates variation in cultural components, leading to cascades of transformations, and thereby to new problems and opportunities (Andersson et al. 2014a; Lane 2016). Second, while this new institution arises as a result of human problem-solving capabilities, there is no evidence (nor reason to expect) that ideas about the outcome – an integrated system of cultural knowledge and practices making up a pastoral economy – guided the actions taken (which applies to domestication generally; see e.g. Zeder 2012, 2015). Humans here built an institution they cannot possibly have understood, they integrated it into a larger cultural system (that they would have understood even less), and it still worked splendidly; see also Lansing's (1987) description of Balinese rice growing communities. Third, the cumulative innovative steps taken did not represent the selective replacement of sociont variants in a larger population, nor is it reasonable to believe that a population of variant institutions was maintained simultaneously within the community.

One possible SPH interpretation would be to view this (at least partly) as a developmental rather than evolutionary process. That is, to see innovation as the development of societal organization via a process that *in turn* was based on heritable cultural information, such as via what Heyes (2018) describes as "cognitive gadgets"; see also Ardila (2018), with writing and mathematics used as examples. Compared with biological counterparts, the degree of sociont developmental plasticity would be exceptional, but, then again, the affordances of a cultural individual would be very different from those of a biological organism. Cultural systems could mediate and organize the behavior of hominins (via their ideas), which would mean that a developmental process could be built upon sophisticated behavioral flexibility. Mechanisms for altering phenotypic expression via a flexible developmental process has clearly been strongly selected for, and has played an important role, in biological evolution (LaFreniere and MacDonald 2013; Sterelny 2011; e.g. West-Eberhard 2003). Andersson and Törnberg (2019) argued that one of the major advantages of an environmentally responsive and integrated cultural system would have been that it could leverage the high flexibility that generally is a trademark of great ape behavior (e.g. Malone, Fuentes, and White 2012; Ungar, Grine, and Teaford 2006); see also e.g. Fogarty et al. (2015) and Fuentes (2017b). That proposition dovetails with the "variability selection hypothesis" (Grove 2011b, 2011a; Maslin et al. 2014; Maslin, Shultz, and Trauth 2015; Potts 1998, 2012) which argues that high levels of environmental variation during the early Pleistocene would have strongly favored any ability to rapidly reconfigure one's behavior.

If so, the main targets of sociont selection and adaptation would not be the detailed expressions of culture, but highly basic cultural systems that underpin institutions and harness the capacity of our large brains (Andersson and Törnberg 2019:86). Systems like these would over time co-evolve with *Homo* to form hybrid systems where genetically and culturally inherited elements would be closely intertwined, making it impossible to classify such systems as either fully genetic or cultural. The evolution of language provides an example of such a system. Genetic changes in hominins enabled the evolution of language. Language itself can then evolve, with selection acting on both words and on entire language systems. Moreover, language shapes human behavior, as it mediates communication and facilitates cooperation (Szathmary 2015). For example, the people at Aşıklı Höyük would have been in a position to embark on their transformation into a Neolithic society (once facing Holocene conditions; e.g. Richerson, Boyd, and Bettinger 2001) because earlier cultural communities (and hominins) in that lineage had accumulated, over hundreds and thousands of millennia, a richer and richer system of tools for dealing successfully with environmental change in general.

5.3 Third difference: lower-level selection

Cultural evolution as selection acting on populations of variants of cultural components, that arise and spread within the cultural community, is a well-researched and central theme in cultural evolutionary studies (Boyd and Richerson 1985, 2005; Cavalli-Sforza and Feldman 1981; Durham 1992; Mesoudi 2007, 2011). This raises the question of how much selection operates also on lower-level cultural components, and how this squares with the notion that cultural group selection would have suppressed lower-level selection during an ETI?

We have identified multiple mechanisms that inhibit lower-level selection, as many of the individuality criteria correspond to mechanisms that promote higher-level selection and/or reduce lower-level selection (Hanschen et al. 2017, Clarke et al. 2013). No mechanism is perfect, and despite these mechanisms, lower-level selection could still be occurring within the sociont, as it does within biological individuals. For example, selection on genes is not completely suppressed in cells (see e.g. Ågren 2014), so the notion of an ETI does not mean that lower-level selection is strictly eliminated.

Another possibility could be that cases of lower-level selection could belong to mechanisms that increase the capacity to respond to the environment.

There are two major examples of biological organs that operate as Darwinian systems based on staged and adapted implementations of "blind-variation-selective-retention" (BVSR; Campbell 1960): the adaptive immune system and the brain (e.g. Changeux 1985; Edelman 1993; Fernando and Szathmáry 2009; Michod 1988). The function of these organs is precisely to provide the biological organism with capabilities for responding to the environment on time scales that are too short for genetic adaptations to be able to deal with them. For example, creativity, learning and the ability to survive the onslaught of pathogenic microorganisms with much shorter generation times.

5.4 Fourth difference: boundaries and manifestation

Biological individuals tend to be physically cohesive, and individuality criteria such as *Spatial/temporal boundaries* and *Indivisibility* are easy to interpret in terms of physical boundaries. The sociont, however, must be imagined largely in other spaces, such as social and ideational spaces. Are such boundaries in the sociont realm equivalent with those in biology? We described sociont boundaries in Section 3.2 but expand upon our discussion here with a tentative description of how a sociont would manifest.

On the basis of the analysis in this paper, we propose that the phenotypic manifestation of the sociont may be pictured as a stationary and organized pattern of behaviors, cultural products, and environmental modifications – coincident with, and maintained by, but not identical to, a social community of hominins. It would be generated and maintained by the dynamical and parallel expression (by hominins) of cultural components, most of which are likely tacit. This emergent pattern would unfold in time and space by the expression of cultural components, regulating the expression of other components (within and between brains) via social interactions, cultural products and environmental modifications. Expressed cultural components would act by modulating hominin behavior via psychology, cognition and meta-cognition.

The stationary structure of this dynamical pattern may be conceptualized schematically (in the manner of an organizational chart) as a nested hierarchy of functional sub-systems – such as for hunting, fishing, tracking, knapping, pyrotechnology, but also strategies for teaching, distributing resources, resolving conflicts, and so on. This organization may be unpacked all the way into the individual brain, where culture interfaces with our psychology and cognition. In terms of extent, this system reaches only as far as its social interactions – i.e. it has a boundary, and the nature and extent of this boundary is evolvable as a part of the system itself.

Moreover, the above description of the sociont potentially dovetails with other models of the dynamics and organization of culture within as well as between cognitive agents.

For example Heyes (2018) describes "cognitive gadgets" as not only functional but also regulatory systems, acting within the brain to form adapted systems from highly domain-general innate components. The autocatalytic network model by Gabora and Steel (2017, 2020) sees learning and creativity as a result of self-organization in mental representation networks, governed by adapted features of the process. They suggest a potential extension of these dynamics to the social level, which could coincide with the above envisioned intra-sociont dynamics, whose mechanisms could be shaped by sociont evolution (or mutualistic sociont-hominin co-evolution.)

Models depicting emergent "group cognition" in networked human cognitive nodes, organized and mediated by culture, have been proposed by several authors (e.g. Coward and Grove 2011; Gallagher 2013; Grove and Coward 2008; Muthukrishna and Henrich 2016; Read 2020), including models where culture and its products themselves are depicted as part of an "external mind" (Clark and Chalmers 1998; Menary 2010); see Theiner (2014) for a review. Cultural niche construction focuses on complex causal feedback loops between cultural behavior and persistent environmental features (Laland and Brown 2006; Laland and O'Brien 2015; Smith 2007), and networked, recombining and cascading features in general are central in many theories of innovation in modern and ancient sociotechnical systems (see e.g. Andersson et al. 2014a; d'Errico and Colagè 2018; Geels 2002; Hughes 1986; Lane 2016; Schiffer 2005; Wimsatt and Griesemer 2007).

The description also recalls several models of biological innovation and organization in a recent family of models often referred to as the "extended evolutionary synthesis" (e.g. Feldman et al. 2015; Jaeger, Laubichler, and Callebaut 2015; Pigliucci and Müller 2010); for its applications to culture see e.g. Andersson et al. (2014a), Fuentes (2016, 2017a), Smith et al. (2018), and Zeder (2018). Gene regulatory networks in biological development (e.g. Arthur 2011) exhibit dynamical and evolutionary similarities with socio-technical innovation (e.g. Erwin and Krakauer 2004). Also, the extension of genes, via social interactions, to group-level adaptations in social insects (via tactile and chemical signals as well as by sensing of persistent modifications of the environment) leads to the formation of a biological organismal unit that also challenges the view of organisms as physically bounded and contiguous entities (Dorigo, Bonabeau, and Theraulaz 2000; Kennedy et al. 2017; Queller and Strassmann 2009).

5.5 Future directions

Sociont-level meta-evolutionary functions (heredity, reproduction, boundaries, and, later, development and conflict modifiers) are here claimed to have arisen from coincidental precursors in the social protocell (Section 2.2). If systems can be found and demonstrated to be adapted to these functions, that would have high diagnostic value (see Section 3.4.2). The concept of 'organismality' (e.g. Queller and Strassmann 2009; Strassmann and Queller 2010; West and Kiers 2009) represents an attempt to understand organisms in the abstract and may serve as a useful starting point for further developing and testing the organism analogy implied by the SPH.

By proposing that culture emerged as an evolutionary individual, the SPH revises our understanding of the structure of human life and evolution. Future work should examine interactions between the sociont and human traits such as cooperation, altruism, and language. The nature of these interactions must be worked out via models and via revisiting frameworks and concepts such as those mentioned in Section 5.4, including models of co-evolution between *Homo* and cultural systems (e.g. Colagè and d'Errico 2018; Durham 1992; Hare 2017; Herrmann et al. 2007; Laland 2018; Laland and O'Brien 2015; Smith 2007).

Additional work should focus on investigating whether marginal institutions in *Pan* exist. These marginal institutions, should they exist, could provide models for the earliest stages of the evolution of human integrated cultural systems. Such systems could emerge if combinations of socially learned behavior were strongly adaptive on the community level, but without the open-endedness argued to apply to big game carnivory. Read (2012:99–104) for example describes substantial intra-species regional variability in group behavior in *Pan*, such as in how border patrols are organized, without evident genetic differences to explain these differences.

Finally, social protocells should be formally modelled to explore what assumptions are needed for the postulated links between the entities (e.g. in terms of fitnesses of traditions, hominins and communities) to operate as claimed, and to explore the range of phenomena that result. Under which conditions can features that promote group selection be selected in that way?

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