RESEARCH ARTICLE

Social cognition and human aesthetic niche—the evolving human cognition as a participant of human niche construction [version 1; peer review: awaiting peer review]

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Abstract

Aesthetic phenomena have been intertwined with the life of humans to a significant degree that is not observed in non-human animals. The complexity and subtlety of it have long been regarded as one symbol of human's exceptional cognitive power. This power can sometimes be misrepresented by a view that regards human aesthetic behaviours as innate/encoded and automated settings that are brought along with the human brain. In scenarios like this, the naturally selected brain takes up a role as some super explanator—by appealing to the configurations of the neural connectivity as reasons/causations for observed phenotypic traits. Therefore, this line of thinking can sometimes obscure the role played by the sociocultural background in affecting those configurations. By drawing upon the notion of niche construction, I will propose a nature-nurture coevolving framework for understanding human cognitive evolution. It will be argued that the evolutionary trajectory of human cognition is heavily defined by and is, therefore, better understood through the lens of a human cultural niche and of contextualised/context-dependent expressions of human behavioural traits. This view will be delivered by highlighting the dynamics between selective pressures and the differential expression of human phenotypic traits and acknowledging the evolutionary causal role of human cultural behaviours and practices. Finally, I argue that a major evolution of social cognition was brought about through an aesthetic tradition of the Acheulean and conclude by briefly proposing a potential subject for future study.

The basic research method applied in this article is theoretical deduction. Specifically, a restricted interdisciplinary investigation that concerns academic literature from relevant fields (centring on the topic of niche construction) of archaeology, evolutionary biology and human cognition was used. Furthermore, through a process of assessing and identifying of plausible evidence, the abovementioned arguments of this study are generated.
Keywords
Aesthetic niche, cognitive evolution, cultural evolution, gene-culture coevolution, human self-domestication, social cognition, niche construction theory

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1. Introduction

Among the known animals on earth, modern humans are believed to have the most complex arrangements of cognitive abilities. Those abilities include, e.g., abstract reasoning, hierarchical language system, long-term memory, self-awareness, shared intentionality, etc. The unique potency of human cognition is sometimes represented by the knowledge of perhaps the most typical trait of humans, an unparalleled computing device, an exquisite problem-solving system, and a remarkable biological adaptation—the human brain. This human-unique equipment possesses a myriad of functions that are crucial for human survival (e.g., emotion processing, selective attention, memory retrieval, motor control, etc.). Usually, many of these functions are organised in different ways to bring about other higher-level functions involved in language using, tool making, and social cognitive tasks encompassing the use of theory of mind, recognition of group identity, social signalling and so on. Together, at the behavioural level, these functions give rise to those phenotypic traits that are conspicuously human—e.g., behaviours based on moral knowledge or local norms, and artistic behaviours such as painting or music-making. It is with this general understanding, the evolution of human cognition is extensively explored, through topics aiming at specific patterns in human behavioural diversity, by researchers from diverse fields ranging from archaeology, and cognitive neuroscience, to evolutionary biology, psychology, and philosophy.

More specifically, research topics focusing on our distinct Homo ancestors have produced rich resources for understanding the evolution of cognition in prehistoric times. For instance, the study on Neanderthal’s life mode and caring behaviours (e.g., Spikins et al., 2014, 2019; Mondanaro et al., 2020) have provided us insights into how possible cognitive adaptations might have evolved under challenging conditions within the North Temperate Zone. To push further into the distant past of the human lineage, studies based on the longest known technological tradition (i.e., the handaxe making tradition) of the Achulean industry, have also suggested that significant episodes of cognitive evolution must have taken place throughout over 1.5 million years of development since~1.78million years ago. To put it very briefly, these studies imply that plausibly by the Late Achulean (about 500,000 to 300,000 years ago), and before the advent of Homo sapiens, the hominin cognition had evolved with capacities by which complex behaviours, such as systematic large game hunting, efficient teaching and learning (supposedly a quasi-apprenticeship system), multi-stage tool making, or even aesthetic practices, were initiated and sustained (e.g., Stupart, 2007; Currie, 2011; Hewlett et al., 2011; Hodgson, 2011, 2015; Dominguez-Rodrigo et al., 2012; Layton et al., 2012; Hiscock, 2014; Sinclair, 2015; Dira and Hewlett, 2016; Boyette and Hewlett, 2017; Diez-Martín, et al., 2018, 2019; White and Foulds, 2018; White et al., 2019; Currie and Zhu, 2021).

Meanwhile, from a more proximate perspective, with the help of experimental methodology (e.g., neuroanatomy and neuroimaging), especially the functional magnetic resonance imaging (fMRI), researchers now can probe into human cognition in a quantitatively more precise way. This is usually done through experiments relying on human participants and comparative experiments between humans and other primates (e.g., chimpanzees and bonobos). However, for our current concern about human cognitive uniqueness and its evolution, recent studies have generated intriguing implications. That is, while comparative studies have pointed to the fact that we can reasonably identify many comparable (analogous) cognitive functions in non-human primates, the differences thus become explanatorily important.

For example, it has been argued that the white matter in human brain has been expanding disproportionately (e.g., Gazzaniga, Ivy, and Mangun, 2014; Donahue et al., 2018). Compared with other primates, human prefrontal cortex shows a much higher constituent ratio in its white matter (which is mainly made up of axons) than in the grey matter (which consists of large bodies of cells). Considering the significance of the prefrontal cortex for human cognition, therefore, this disproportionate development of white matter seems to imply some human-specific evolutionary selection. In another experiment, Donahue et al. (2018) have carried out detailed measurements comparing the absolute volumes of the prefrontal cortex, grey matter, and white matter among human participants (n=60), chimpanzees (n=29) and macaques (n=19)1. The outcomes have demonstrated that the ‘white matter underlying human PFC is particularly large compared with nonhuman primates’ (Donahue et al., 2018, p.E5188). Again, since those axons’ (the white matter’s only constituent) job is to process and send nerve signals from and to other body regions, the fact that humans have disproportionately highly developed white matter favours the speculation that strong selective pressures must have come from some persistent need for a refined, well-tuned, or sophisticated synergy that better exploits and connects various other parts of the brain and body. In the next sections, it will be suggested that human cumulative cultural niche construction is a source of selective pressures on brain connectivity. Here I quote Gazzaniga, Ivy, Mangun, “the cognitive

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1As the data shows: the proportion of prefrontal cortex gray matter for human can be ~1.6 to 1.9-fold greater than for macaques and ~1.2-fold fold greater compared with chimpanzees. However, regarding the fractions of prefrontal cortex white matter-to-total white matter volume, ratios of ~12%, ~7%, and ~5% are obtained respectively for human, chimpanzee, and macaque. Thus, the disparity becomes salient, a 2.4-fold difference between human and macaque, and a 1.7-fold between human and chimpanzee (Donahue, et al. “Quantitative assessment of prefrontal cortex in humans relative to nonhuman primates.” Proceedings of the National Academy of Sciences 115.22 (2018): E5183-E5192).
Another related example is the FOXP2 gene, which is believed to be a key factor for the development of human language ability. Briefly speaking, the FOXP2 gene exerts its power by regulating the expressions of genes that are involved in language using. So, it has long been regarded as crucial for human cognitive uniqueness. However, studies have shown that the FOXP2 gene is not unique to modern humans (Neanderthals and other animal such as some species of birds, too, have the FOXP2 gene), and there is no recent selection for it (Krause et al., 2007; Gazzaniga, Ivry, and Mangun, 2014; Atkinson et al., 2018). According to Gazzaniga, Ivry and Mangun (2014, p.503), the FOXP2 regulates a wide array of genes that are involved with e.g., morphogenesis, intracellular signalling, neuron outgrowth, and learning, etc. Thus, just as the above example has implied, what might be the case is not some single gene that alone codes for unique human linguistic behaviours. Nevertheless, what really leads to the uniqueness here is probably a set of context-dependent factors that specifies the regulatory rules for the FOXP2 gene. In other words, it was the contingent interactions between the human niche and the expression of many other phenotypic traits (more basic ones) which eventually gave birth to the higher-level phenotype of language using.

To summarise the introductory part, firstly, based on the evidence at hand, researchers have argued that complex cognition (manifested through the material cultures such as the Acheulean industry) might well have existed in the distant past of the human lineage, way before the presence of Homo sapiens. Secondly, the above studies of neural and genetic substrates of human cognition have indicated that, in the evolutionary sense: 1. There might be certain elements in hominin’s everyday life (which are demanding in terms of neural cross reference and integration of sensory information) that motivate complex organization of behaviours; 2. These elements might have managed to get involved in the way of subsistence of different hominin societies through mechanisms like social transmission; 3. Thus, they became causally accountable in explicating the course of human cognitive evolution, e.g., by inducing effects of Baldwinisation. That said, the significant role of culture has been brought to the foreground. Such an implication, by acknowledging a deep interweaving relation between cognition and culture, echoes with the recent findings of theories (e.g., niche construction theories and epigenetic theories) which advocate that cultural factors can produce stably transmitted phenotypic traits at the population level, emphasises the possibility that human cognition (and human evolution in general) is, to a considerable extent, culturally driven and flexible.

This current research will adopt an interdisciplinary perspective, with a generally deductive manner of theoretical analysing and integrating, that draws upon key works in evolutionary biology and archaeology to touch on the topic of cognitive evolution. In short, the general topic of human cognitive evolution will be addressed by proposing an inclusive evolutionary framework on human aesthetic tradition—one that acknowledges an aesthetic niche. That is, to see human aesthetic activities/practices as a mode of niche construction.

That said, before such a framework could be obtained, this research will examine:

1. The notion of niche, the theory of niche construction, and the postulated relations between niche construction, organism evolution, social learning, and cultural evolution. In this regard, key works by Laland (e.g., 2014), Olding-Smee (e.g., 2003), and others will be discussed. Such a discussion will serve as a foundation for the conception of ‘human aesthetic niche’.

2. Based on 1., the deep history of human aesthetic culture/tradition, as an important aspect of human aesthetic niche that affects cognitive evolution, will be explored. Being perhaps a stone technology that had persisted the longest time span in human lineage, the Acheulean handaxe tradition will be focused upon. Specifically, evidence from key literature on the economics in handaxe manufacturing (e.g., Lycett et al., 2016; de la Torre, 2016; Pargeter, Khreisheh, and Stout, 2019), transmission of skills in palaeolithic groups (e.g., Hiscock, 2014; Diez-Martín et al., 2018), handaxe morphology (e.g., Beyene et al., 2013; Key and Lycett, 2017a; Shipton, Clarkson and Cobden, 2018; White and Foulds, 2018) will be discussed and incorporated to generate claims about the evolution of social cognition in Acheulean times.

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3In a nutshell, the Baldwin effect refers to the phenomena in which some derived characteristic in some organisinal population becomes more innate and less sensitive to environmental conditions (further discussion will be given in Section 3).
4By ‘culture’, I intend the whole chain of evolutionary dynamics that it entails—e.g., cultural innovation, social learning, cultural inheritance, and cultural evolution, etc.
In the following sections, I will first (in Section 2) take a step back and provide a general theoretical framework of evolution that sustains both the cultural and the biological contribution. It will be argued that the uniqueness we see currently in our cognitive prowess is likely to be an evolutionary consequence of the constant interaction between our unique reliance on the accumulating human culture and selective mechanisms. Then (in Section 3), I will offer discussions on aesthetic activities such as the appreciation of Acheulean handaxes, arguing that the cognition involved in aesthetic activities is mediated by this biocultural framework.

2. Making our conception of human evolution more inclusive

This section intends to articulate the hybrid nature of human evolution and to suggest a more inclusive framework for understanding human cognitive evolution.

To do this, I will appeal to the notion of niche construction. But before that, let us recall a more classic framework of evolution, the Modern Synthesis. Put in a few sentences, the modern synthesis is a view through which stably transmitted phenotypic traits of an organism are treated as, in essence, genetic traits (Danchin et al., 2011; Scott-Phillips et al., 2014; Laland et al., 2015). Or to put it another way, genetic variations and corresponding genetic inheritance should present as a prerequisite condition for any observed cross-generationally preserved phenotypic traits (with cognitive patterns being an important type).

However, as is well-known, at the ontogenetic level, phenotypic traits can be derivable. Through mechanisms such as social learning and through molecular level mechanisms such as epigenetic methylation, the brain (neural connectivity) exhibits outstanding cognitive flexibility. That is, neurological changes could occur when individuals are exposed to major changes in their selective environments (e.g., individuals who experience long-term exposure to alcohol can develop a dependence which could be identified cognitively and behaviourally, but clearly in this case, the sociocultural background could play some part, in addition to one’s predispositions to alcohol³). A question can be asked, could traits like this (and other phenotypic traits that are socially learned or culturally triggered) become inheritable? The answer is possibly a ‘yes’. Recent studies have identified cases of trans-generation inheritance of derived traits—e.g., the specific way of tool using in human-raised crows (Danchin et al., 2011); an inherited aversion of specific olfactory stimuli among experimental rats (Dias and Ressler, 2014); similarly, acquired taste aversion is identified in fruit flies (Heyes, Chater and Dwyer, 2020); high level expression of lactose tolerance in human populations with a dairy tradition, and the increased copies of the salivary amylase genes in agricultural societies (Laland and Sterelny, 2006, Laland et al., 2014, 2016; Menary, 2014; Papineau, 2005b; Perry George, et al., 2007; Scott-Phillips et al., 2014). These findings have called the Modern Synthesis into question. It is important to see not just the underlying configurations of the genetic inheritance, but also the dynamics in the sociocultural background which contributes to these changes, if we are to gain a fuller explanation for human cognitive and other phenotypic traits (e.g., an alcohol dependence and related behaviours).

2.1 The phenomena of organism niche construction and its evolutionary consequence

The worries for the Modern Synthesis have stimulated the development of alternative theories in the field of evolutionary biology. As evidence grows, the niche construction theory has been gaining traction recently (Laland, 2008, 2013; Laland et al., 2014, 2015, 2016). ‘Niche construction’, refers to the phenomena where organisms actively modify their own and others’ niches (Day, Laland, Odling-Smeee, 2003; Odling-Smeee, Laland and Feldman, 2003; Scott-Phillips et al., 2014; Laland, Matthews, Feldman, 2016). Moreover, since such modifications usually have the potential to influence selective pressures in the environments, novel episodes of evolution could incur due to significant changes in selective pressures, i.e., niche construction induced evolution. In this sense, the idea of niche construction, by taking the fact (that is, through their environment-shaping activities, organisms can actively affect the evolutionary trajectories of their own) into consideration, brings to the foreground this more inclusive nature of evolution. As a result, for many who advocate a fundamental role of niche construction for organism evolution, this perspective takes up the name ‘niche construction theory’ or ‘NCT’ (Laland and Sterelny, 2006; Kendal et al., 2011; Laland and O’Brien, 2011; Odling-Smeee et al., 2013; Laland et al., 2014, 2015; Laland, Matthews, Feldman, 2016; Laland, Odling-Smeee, and Endler, 2017).

Other than the different senses in which the term ‘niche’ is previously used (Grinnell, 1917; Elton, 1927; Hutchinson, 1944, 1957; Holt, 2009), when used in NCT, the notion ‘niche’ is defined as, ‘the sum of all the natural selection pressures to which the population is exposed.’⁶ This is a broad and inclusive definition, which also captures the evolving nature of a

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³Early developmental stage alcohol use is believed to be another possible cause as well. Other than this, scholars have suggested that cultural should be hold responsible for many addictive disorders. Also, it is still an unsettled question that whether we should regard addictive disorders as diagnosable brain diseases or not. (For further discussions on this issue, see for example Lesnner, 1997; Fouldy and Savulescu, 2006; Levy, 2013; Pickard and Pearce, 2013; Sinnett-Armstrong and Pickard, 2013; Culbert, 2014).

niche. It allows for the sum total of the conditions where a species in question, through constant interactions with the natural context, maintains the development and persistence of its own. By taking this perspective of regarding species as subjects engaging in different niche constructing processes, the following points become important:

1. Evolution to a considerable extent is subject to a relationship, which is dynamic and mutual, between organisms and their surroundings—a situation in which organisms are always constrained by selective factors in the environment, and in respond to those factors, alterations to such environments are always made by those organisms as well.

2. The constraining/selective environmental factors and the organism’s acts that elicit novel constraints play the crucial roles that usually produce evolutionary outcomes.

3. Selective pressure is the agent through which these two parties form an evolving equilibrium.

2.2 The human cultural niche

Examples of niche construction in the organismal world are numerous. For current purpose, I will leave some of those much-discussed cases—e.g., of yeast, earth worms, hermit crabs, and beavers (Laland et al., 2016; Bateson, 2017)—aside and focus on the human niche, especially, the cultural niche construction in human populations.

As a matter of fact, primates do seem to have employed various culturally derived ways of niche construction. For instance, in wild chimpanzee groups, the behaviour of making a primitive form of ‘sponge’ from leaves is regularly found. This behaviour buffers the need of water consumption and is believed to be socially learned (Whiten et al., 1999; Hobaier et al., 2014; Lamon et al., 2018). Meanwhile, the presence of Japanese macaques’ food-washing activity is suggested to be another example of a behavioural pattern which get transmitted cross-generationally through a cultural manner (Kawamura, 1959; Kawai, 1965; Scheurer and Thierry, 1985). Nevertheless, human populations, still, exhibit an unparalleled level of dependence and exploitation on the wealth of cultural resources in respect of their niche constructing activities.

Whenever we think of ourselves (modern humans), it occurs intuitively and obviously that modern humans are probably the only species that not only modifies its environments in a notably comprehensive scale, but also relies so tightly and heavily on cultural practices in achieving those modifications. With the help of technology, modern humans have been carrying out planet-level cultural niche construction. The earth’s landscape has been profoundly transformed into cities, farmlands, or industrial lands. Natural resources are being transported and re-distributed worldwide through oil tankers, airliners, passenger trains etc. The development in telecommunication (e.g., internet, smartphones, personal computers, etc.) largely enables to a much more efficient exchange of human knowledge across continents, regions, and nations. Furthermore, by sending satellites and research stations, the human culture is accelerating its pace into the outer space.

Apart from the above overview of the magnitude of human cultural niche construction is and how it could have permeated nearly every aspect of human life, there is well-tested evidence showing human-led cultural influences on human genetics. Some famous examples include the spread of phenotypic traits of lactose tolerance, malaria resistance, and starch digestion in human populations (Perry et al., 2007; Rendell et al., 2011; Laland and O’Brien, 2011; Laland, Matthews, and Feldman, 2016). These cases have pointed to a possible fact: human culturally acquired behaviours can lead to non-random evolutionary consequences through a two-way mechanism that acts bilaterally and simultaneously—the buffering of specific selective pressures on one hand (e.g., the pressures for stable food sources that buffered by regular intake of dairy products or starchy crops), the emerging of novel pressures brought about on the other hand (e.g., selection for increased lactose tolerance or amylolytic capacity).

2.3 Cultural selection and cultural evolution

What has been said above has focused on just one type of the outcomes of cultural niche construction: that is, for a cultural practice, the process of cultural niche construction can lead to its refinement and stabilization over time. But when a cultural practice is put into a network of cultural practices like in the real-world condition, another type of outcome that bears equal evolutionary potency is the impact this niche constructing practice may have upon other related practices.

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7 Let us say, for some species ‘X’, the ‘X’ niche therefore incorporates the sum of interactive possibilities or potentials existing in the accessible ecosystem that could affect ‘X’ species’ fitness over time.

8 For clarification, the term ‘cultural niche construction’ used here refers to the aspect of human niche construction that depends on human cultural resources.
Behavioural patterns that are culturally acquired and transmitted usually cause changes in evolutionary fitness of other cultural traits (by indirectly mediating the course of transmission and the expression of relevant genes). On the analogy of the dam-building beavers’, human behavioural traits, when they are organised and expressed through habitual ‘practices’ or ‘traditions’, often exert selective effects on other phenotypic traits that are not so immediately related to the practice itself. Socially learned patterns like, for instance, local norms related to mate choice, religious or superstitious activities, specific technological practices, or even preferences in food choice, could produce far-reaching (but consequential) influence on many other behavioural patterns that coexist in the same community. Particularly, when these culturally led traits are learned rapidly among industrialized human societies (with the support of technologies and education systems), and when paired with mechanisms such as sexual selection, or assortative mating, they produce strong culture-grounded selections in human population. From this aspect, we can see two notions are relevant: cultural selection and cultural evolution.

Cultural selection emerges when: 1. Some adaptive phenotypic trait is socially learned and spread among individuals of a population; 2. Major sources of selective pressures to which this population exposed stay stable; 3. This trait can be traditionalised, and the cumulative cultural inheritance could then lead to scaffolded learning; 4. Cultural selection for this trait appears.

Cultural evolution, accordingly, is the process in which diverse kinds of phenotypic traits, that are subject to persistent cultural selections, are manifested through behaviours, practices, and traditions of cultural niche construction of a population. What is so important here is that, considering evidence of niche construction we have so far (e.g., the spread of human alleles due to human farming, the dam-building regulated beaver physiology and morphology), it is reasonable to expect that, in the long term, cultural evolution could exert selective pressures on a wider spectrum of genes. If a cultural practice somehow is expressed (or inhibited) in a stable manner, certain genes (partially underlying that practice) can incur either an enhanced or a suppressed expression: think of the differential expressions of amylase genes that contribute to human starch digestion that depend on different levels of the cultural practice of starchy crops farming. At the same time, regardless of whether it is an over-expression or a suppression, the same practice can still affect the expression and the adaptive value of other genes. As a matter of fact, the current human life is inevitably filled with numerous products of the Digital Age. Through a systematic integration with individual’s life, this process of digitalisation and the novel selective pressures it induces might have left its mark in our species biologically. Indeed, there are recent studies which have suggested a correlation between increased risk for suffering an intervened early-stage brain development, ADHD, or depression and habits that contribute to prolonged screen time on digital devices (Madhav, et al., 2017; Hutton et al., 2020). However, to determine whether this correlation is a causal one or whether such culturally acquired traits have produced inheritable cognitive changes, further research is needed.

3. Human aesthetic niche and the deep history of cultural intervention in cognitive evolution

In line with what discussed previously, for species that depend heavily on their cultural niche, the cultural intervention is expected to play a leading role in driving the gene-culture coevolution process. Therefore, it is certainly not a bold guess to assume that modern human’s evolution has probably been (and will continue to be) mediated by its cultural activities. This, as I will suggest, had happened in the deep past of our hominin ancestors’ societies dating back to perhaps the Lower and the Middle Palaeolithic.

By relying on the technological practice of handaxe making starting from ~1.78 million years ago, this cultural behaviour gradually obtained a new role in social signalling through a joint force with existing aesthetic niche and a process of Baldwinisation, and eventually (throughout a over 1 million years’ time span of development), had led to presumably the earliest presence of a complex form of human cognition, i.e., a culturally grounded aesthetic social cognition. To have a better grasp of this picture, a clarification on several key notion is needed.

3.1 Human aesthetic niche and the Baldwin effect

The notion ‘human aesthetic niche’ (used in a general sense, including that of our Homo ancestors) is not to be thought as a subset of the human cultural niche. In line with our discussion of the notion ‘niche’ and ‘niche construction’, the notions of ‘aesthetic niche’ and ‘aesthetic niche construction’ can be defined accordingly as: the total of the selective pressures to which a human population is exposed during the process of aesthetic niche construction, and the specific way of niche construction that relies on human aesthetic resources. Although it is usually the case for modern humans that an example

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9The behavioural mode of building dams has brought about drastic changes to beaver’s niche by placing a semi-aquatic environment, which is an outcome of an ecosystem full of dams, at the centre of the species. Not only have such surroundings (directly) modified selective pressures on dam-building relevant genes like those expressed by the evolved trait of beaver’s webbed feet, but also (indirectly) affected, as I quote Laland (2004, p. 317), ‘genes that are expressed in quite different traits, such as beaver teeth, tails, feeding behaviour, susceptibility to predation, diseases, and life history.’
of aesthetic niche construction constitutes an example of cultural niche construction. However, we should only see the human aesthetic niche as in effect a sub set of the total ecological niche of human, which overlaps (though largely) with the human cultural niche.

This is supported by the studies of those who advocate an evolutionary psychological theory for human aesthetic mind. In other words, the fact that humans inherit a repertoire of aesthetic sensibilities and preferences for characteristics of the natural world and of the human body. Related topics that are well-tested include: e.g., preference for savanna-like landscapes, above-average body height, a ~0.8 waist to hip ratio, or the averageness of faces, etc. (there is a large body of research on such issues, see e.g., Miller, 2001; Fink and Penton-Voak, 2002; Rhodes, 2006; Buss, 2008, 2016; Dutton, 2009, 2010; Miller and Maner, 2010; Rusch and Voland, 2013). In this regard, we see that aesthetic niche construction could happen outside (i.e., with no reference to cultural resources) the overlapping area with the cultural niche. Besides, as implied by the general dynamics of niche construction, we should not exclude the possibility for fluidity/ flexibility since there is no hard line between them.

Roughly, the Baldwin effect is often used to denote the process during which behavioural traits that were initially derived gradually become internalised among individuals of a population (Sterelny, 2004; Papineau, 2005a; Crispo, 2007). An episode of Baldwinisation could happen, theoretically, on following conditions: 1. Some change in selective pressures is caused, making a specific behavioural pattern (let us call it X) adaptive. 2. Such change takes place through a non-radical way, and it persists long enough so that a small portion of the population could acquire X through individual trial and error. 3. Recognition of those ‘fitter’ individuals thus promote social learning of X, which stabilise X as a species-specific mode of behaviour. 4. A stabilised state of performing trait X induces positive selection for elements (at both the phenotypic level and the genotypic level) that facilitate the acquisition of X, thus, gradually makes X innate. As Sterelny describes, this effect is ‘a transition from development contingent on rich and specific environmental signals to development which is insensitive to environmental variation.’ Indeed, there can be an evolutionary trade-off happening between the cost of learning and the benefits of making the object of learning encoded. When benefits outweigh the cost, this transition could ensue. In spite of this, the Baldwin effect is more like a possible outcome of niche construction. Niche construction provides the major source of adaptive traits, meanwhile the process of Baldwinisation relies on stable external inputs —i.e., persistent selective pressures—to allow the internalisation of the target traits. For sure, niche construction results in modified pressures which usually contribute to the retention of some derived behavioural pattern, but it does not necessarily make it encoded.

3.2 Acheulean handaxe making and social cognition within an aesthetic tradition

The Acheulean industry is a Palaeolithic technological tradition that can be characterised by its continued reliance on the production of a distinctive type of stone tool, the ‘handaxe’. With the development of this tradition, especially from the middle to the late Acheulean, sophisticated handaxes were produced in large quantities. Among them, characteristics of obvious aesthetic concern—e.g., high level of symmetry, well-arranged scars, finely processed edge line, even design features such as hollowing—are found.

Based on the relation between the two classes of niche (aesthetic and cultural) we have just mentioned. The reason why this handaxe making tradition is so important is that: through what we have restored about the development of this material culture, the generations of making and refining (presumably from ~1.78 million years ago to ~500,000 to 300,000 years ago) of this practice had led to an emergence of a profound social learning system, which then gave birth to a culturally grounded aesthetic cognition—a mode of cognition, I suggest, that might be the ancestor of the kind we have when we appreciate arts.

For sake of a more focused and concise argument here, I will leave aside specifics such as technological issues in specimen evaluation and provide key milestones that would sustain this proposed scenario of cognitive evolution.

At its very beginning, there must be a transition from the previously dominant form of stone tool—the Oldowan choppers and flakes—to Acheulean handaxes. That is, there must be selective pressures that were buffered by the use of handaxes.

Modern humans inhabit a highly aestheticized world in which aesthetic niche construction is deeply intertwined with cultural niche construction (e.g., Currie, 2012). Think of artefacts such as body decorations (e.g. tattoos, clothes, hair dress), architecture (e.g., museums, galleries, stadiums), many other daily objects (e.g., tools, gifts, commercial ads, food packages) and the fine arts. This is also true in non-industrialised societies of present day: e.g., the ‘Potlatch’ tradition among indigenous societies of the North America (Boas and Hunt, 1897; Piddocke, 1965; Ringel, 1979; Harkin, 2001), the Gerewol festival celebrated by the Wodaabe people of Niger (Beckwith, 1983), or the ‘Sing-Sing’ gathering and the ‘Moka’ exchange of Papua New Guinea highlanders (Strathern and Strathern, 1971; Feil, 1987; Strathern, 2007).
which enabled the handaxe to outperform Oldowan tools in the first place. According to studies on handaxe practicality (Galán and Domínguez-Rodrigo, 2014; Key and Lycett, 2017b), handaxes are considerably more efficient when dealing with heavy-duty tasks such as butchering (in which a handaxe could be used as a multi-purpose tool for de-fleshing, cutting, or smashing). Meanwhile, analyses based on animal fossils (Layton et al., 2012) and the identification of the earliest known case of porotic hyperostosis12, a likely marker of habitual meat intake (Domínguez-Rodrigo et al., 2012) both point to the possibility that systematic group hunting could have existed in early Acheulean, thus heavy-duty work might reasonably constitute a significant part of the daily routine of Acheulean individuals.

Secondly, as the handaxe became prevalent, a result of this widely employed mode of niche constructing practice would be a set of strong selective pressures on factors which facilitate the practice of handaxe making. Considering those facts about the costly nature (at both individual and group levels) of maintaining a handaxe making tradition:

1. Making a functioning handaxe is cognitively demanding, even for present learners, it takes years to become an expert (Pargeter, Khreisheh, and Stout, 2019), the maker would need a mental template during the processing, and a set of technical skills to organise, monitor and adjust a long and subtle sequence of actions (e.g., to make centripetal blows on the edge; to keep the striking angle less than 90 degrees to ensure a conchoidal fracture). All these would need to be carried out well to overcome copying errors (Lycett et al., 2016; de la Torre, 2016).

2. On the hand, for handaxe making practice to become stabilised as a tradition, the makers and their societies would also need a substantial volume of other knowledge that is not directly related to the manufacturing process (Hiscock, 2014; Diez-Martín et al., 2018). This would include: a. a basic understanding of practical physics which helps with determining suitable raw materials; b. the knowledge of geological mapping of various kinds of resources (e.g., locations of raw materials and source of water); c. the knowledge of dealing with challenging situations—e.g., the regular need of searching and transporting of raw materials would mean a higher frequency of predator encountering; d. the knowledge of avoiding or coping with physical risks during the knapping—e.g., a wound in hand might lead to severe infection or death, which could eventually affect the sustainability of the group.

3. Apart from 1 and 2, the nature of lithic processing makes it, to some extent unforgiving. The physics of stone leaves little room for mis-conduction especially at the finishing stage where the material is thin. A mistake could destroy the whole time-consuming, strike-by-strike, and risky process of making.

Therefore, factors that buffering these costs (i.e., selective pressures) would be under selection.

It is at this stage, I suggest, that the Acheulean handaxe tradition had promoted the social learning in Palaeolithic populations. For the societies that integrated so tightly with this stone technology of handaxe production, it would be crucial for individuals to become a good handaxe maker, and for the group to preserve and share the valuable knowledge required in handaxe making. Considering the costly nature and the complexity involved in this technology, during the middle to the late Acheulean, a developed social learning system might be in place. Within this system, a behavioural pattern that bonds experienced individuals with other less experienced ones could take place. That is, through a possible teaching-learning relationship, the cost of high-fidelity transmissions of valuable skills and knowledge between individuals and over generations would be decreased. In this manner, a concept/idea of someone being a good teacher/maker could emerge and be recognised in an Acheulean society. The preference for a good ‘teacher’ and the acknowledgement of expertise, would probably lead to a competitive social context: only those who have successfully shown their skills would be treated as the one others could learn from. Eventually, this seemed to have laid the ground for the aesthetic culture we see in those well-made handaxes. In this sense, the exaggerations (e.g., being large in size, having high degree of symmetry) in handaxe morphological traits are to be understood as honest signals.

Furthermore, it is possibly due to the perceptual fluency13 and perceptual bias at the beginning (Hodgson, 2011, 2015, 2019; Flavell et al., 2020) and a level of Baldwinisation (as an outcome of Acheulean aesthetic niche construction) at later time that symmetry became a type-feature (in the vein, an effective honest signal too) of handaxe. According to the studies of this core feature of handaxe—e.g., in general, a chronological increase in handaxe symmetry can be seen based on specimens from sites around the world; handaxe symmetry plays little or no role in terms of handaxe practicality; high

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12 A pathological condition in which one’s bones and related tissues become spongy and porous. The presence of this condition is believed to be a result of anaemia.

13 The phenomenon in which the processing of certain kinds of stimulus generates a subjective feeling of ease. A fluent processing could lead to positive assessment of the stimuli perceived.
level of symmetry in handaxe is more like a deliberate design rather than a by-product of the making process (Saragusti et al., 1998; Machin, Hosfield and Mithen, 2007; Beyene et al., 2013; Hodgson and Verpooten, 2014; Iovita et al., 2017; Key and Lycett, 2017a; Shipton, Clarkson, and Cobden 2018; White and Foulds, 2018)—we can reasonably regard handaxe symmetry as an aesthetic feature.

With evidence at hand, I claim that it could be the case that because of the persistent practice of handaxe making, at least by the middle to late Acheulean, hominins’ societies had become in essence aesthetically and culturally intertwined. It is in those societies, an aesthetic culture and correspondingly, a culturally grounded aesthetic cognition emerged.

4. Self-domestication in Palaeolithic populations?
In the case of human niche construction, one important consequence of human cultural niche construction is the self-induced cultural selection on human population itself. Therefore, the human self-domestication (HSD) hypothesis is consistent with the general framework suggested above.

This hypothesis is about the idea that, like the process of animal domestication, modern humans (by way of conducting purposeful activities that select for prosociality) are domesticking themselves, leading to biological adaptations in the population. Studies have suggested that the presence of a set of morphological, physiological, and cognitive traits in human (e.g., reduction in brow ridge, decrease in facial length, prolonged development period, reduced reactive aggression and cooperative communication, etc.) is caused by this selection (Hare, 2017; Chirchir, 2020; Gleeson, 2020). Based on such evidence, many have suggested that HSD is important in terms of understanding human phenomena such as language (Benítez-Burraco and Progovac, 2020), others have suggested possible causes of HSD appealing to selection against aggression (Hare, 2012, 2017), proactive aggression (Wrangham, 2018, 2021), and neural crest cell development (Gleeson, 2020).

Analogous to what has been discussed in Section 3, by focusing on a specific cultural practice, the feedback loop between pressure-buffering activities and novel selective pressures could significantly modify the social dynamics of a hominin’s society (e.g., a late Acheulean society which exhibits a complex social learning system), favouring a high level of prosociality as well. However, if self-domestication did occur in this case, it would have a cultural root.

5. Concluding remarks
By drawing on the notion of niche and theories of niche construction, and by emphasising the evolutionary significance of human cultural (and aesthetic) niche construction, I suggest that the bio-cultural nature of the evolution of human cognition can unfold in a systematic and unified manner. Cognitive evolution is subject to a reciprocal mechanism in which phenotypic traits are mediating and at the same time mediated by the human niche. More specifically, it is through the concerted reciprocity between a cultural practice relying on stone processing and the mediated environments, a cultural cognition that is also aesthetic appeared for the first time in the human lineage.

Data availability statement
No data are associated with this article.

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References
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