Topics in Cognitive Science

Culture: the driving force of human cognition

--Manuscript Draft--

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Abstract:	It is often, though sometimes only implicitly, assumed that biological/genetic evolution sets neural substrates, that neural substrates fix cognitive abilities, and that cognitive abilities determine the spectrum of cultural practices exhibited by a biological species. We label this view as the "bottom-up-only" view. In this paper we will show that such a "chain of dependence" is much looser than usually assumed, especially as far as recent periods (the last 800,000 years versus the last seven million or more) are considered. We will provide evidence and arguments supporting the idea that cultural innovation may have direct and ascertainable effects both on the cognitive capabilities of populations of hominins (via what we call "cultural exaptation") and on the neural substrates of the individuals in those populations (via what we call "cultural neural reuse"). Together, cultural exaptation and cultural neural reuse may give raise to a plausible general mechanism for cognitive evolution in which culture is the driving force, thus offering a "top-down-also" view of human evolution.
Response to Reviewers:	Dear Fiona, Thank you for the opportunity to resubmit a revised version of our manuscript Culture: the driving force of human cognition. We address below, introduced by an asterisk (*), on a point by point basis, how we have addressed the comments raised by you and the reviewers. As you will see, we have made almost all the changes suggested by you and them, including those concerning the figures. We think that, thanks to the comments and issues raised by the reviewers and synthetized by you, the paper is now much stronger. We hope that the revised manuscript will be accepted by TopiCS as we believe that it is a significant contribution and of interest for a large scientific audience. We look forward to hearing from you With kind regards, Ivan Colagé and Francesco d'Errico P.S.: Please, notice the Ivan Colagè is the first and corresponding author of this article. It appears as the second author in the submission system since the manuscript was

submitted by Francesco d'Errico and the system did not allow to indicate a different first and corresponding author. The order of the authors is correctly indicated in the revised manuscript. Thanks.

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Editor
R1 and R3 are especially enthusiastic and make only minor points. R1's comments regard your stance on various literature; give suggestions to improve the figure; and have a request regarding the SM. The last point (to give a one line summary of each paper) would turn this bibliography into an exceptionally useful resource. My sense is that your Figure 3 is so usefully summative and beautiful that the effort required on the bibliography would be well worth it. I urge you to take this suggestion on. I agree with R3 on the orientation of the Figure, given that in a majority of literate traditions, time moves from left to right.

*See below the changes made to address these concerns

R2 makes astute observations on your characterisation of the bottom-up and top-down views. I concur that the extreme bottom-up view is difficult to pinpoint on particular scholars (you point the reader to reviews that do not seem to speak to human evolution directly), but if the dichotomy is to remain, then you must address this point. One potential solution would be to re-envision your contrast as a continuum. Whichever you choose, please address R2 on this. R2 also remarks on each of the individual cognitive capacities that you present evidence for, and has useful suggestions for strengthening your case. Please implement and/or consider these accordingly in a response.

*See below the changes made to address these concerns

Along with R2, my sense is that the top-down perspective is not as well-characterised as it could be either. R2's opinion is that your genes-culture dichotomy is simplistic, but I think it is simply that there is nuance in your in-between stages to bring out in revision. Editorially, I do think that more explanation of HOW the cultural evolution of cognition works is needed.

*We have added two paragraphs in the Conclusion section in which we explain how we think cultural evolution may work according to the "top-down-also" view, and problematize relationships between genes and culture so to make our dichotomy appearing less simplistic. We also explain that the biological foundation upon which cultural evolution builds up are, according to our review of the archaeological evidence, a characteristic of our genus rather than our species.
In the section beginning "Finally, as for the fourth topic" on culturally-driven evolution, there is a notable omission of the perspectives of Cecilia Heyes. Ideas in her 2012 "Grist and Mills" in Phil Trans Roy Soc, for example, or her recent book Cognitive Gadgets. Similar ideas regarding the cultural evolution of language are apparent in Evans and Levinson 2009 BBS.

*We have added these references. Thank you pointing them to us.

Finally, I have some small comments of my own.
Introduction
The aim of the paper is in the abstract, but it also needs to be stated in the intro earlier (p4 15-17 "A number of empirical findings …").

*We now state the aim of the paper after this sentence

Section 2.1
Figure 3 is a lovely rich visualisation from which many important inferences can be drawn. While references are listed in the supplementary material, please help the reader a little more. In the text justify why the data are presented by region / give earliest evidence for human occupation / state that a number of species are considered here etc.

*We better explain the purpose of the figure, why the data are presented by region, and the number of fossil species considered (a request also made by reviewer #3).

Moreover, lines 52-56 on p.11 are key to understanding this section. For the cognitive science audience, present this information earlier in section 2.1 to show what the purpose of the figure will be. Similarly, lines 35-39 on page 12 will help the reader interpret the figure and can come at the beginning of this paragraph.

*We added a sentence at the beginning of section 2.1 in which we clarify the purpose of the figure and what kind of inferences can be made from it..

Each of the points 1-5 is explained further in text, but perhaps this whole section could be reworked so that the "consideration" is followed immediately by the implications on page 12.

*We have tried to follow this suggestion but ended up with a text that appeared to us less incisive than that of the submitted manuscript.

2.2 Exaptation
Is there an opportunity to either link more closely, OR, demarcate more clearly, your notion of cultural exaptation and that of cumulative cultural evolution?

*We have explained the difference between cultural exaptation and cumulative cultural evolution at the end of section 2.2

If any remarks are not clear, I am happy to clarify and advise further. When resubmitting your revision, please indicate in an accompanying letter how you addressed the various points raised by the reviewers.

Best wishes
Fiona

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Reviewer #1: Dan Dediu

There is very little I do *not* agree with in the paper (maybe this makes me too lenient a reviewer?), and I would argue that indeed most of these ideas are becoming the new "common ground" when thinking about human evolution (not in small part due to the authors' own primary research and theorizing!): this is why I had to go for only a "3" on originality. Nevertheless, I think that it is precisely such papers that help popularize these views outside the specialist community and improve their fit to the empirical data, so I would strongly urge its publication.

I do, however, have some small comments:

p4, 9-12: I don't think that the ASPM/MCHP1 2005 papers are taken seriously in the genetics literature anymore, especially in what concerns their claims about "recent and ongoing" adaptive evolution -- the methodology used (coalescent simulations) is quite open to criticisms and later work seems to convincingly show that while the "old" selective pressures and the geographic patterning are probably real, the "recent and ongoing" ones are probably due to population structure

*We have eliminated the paragraph in question

p4, 14-22: the evolutionary story of FOXP2 is is much more complex that described here, and the authors seem to have missed (or decided not to mention) all the juicy stuff that came out of Svante's lab post 2002 including refining the selective signal on FOXP2 (actually, there might have been at least 2?) and when & why it might have happened...

*We have eliminated the paragraph in question as a detailed review of the FOXP2 is outside the scope of our article p5 23: probably "mechanistic"?

*Corrected

p10 Figure 3: I think the figure might become easier to follow if: (a) there would be some space separating the 4 rows of each innovation, and (b) vertical guides at say each 100k

*We have added vertical and horizontal lines in a darker gray. They help the reader to better identify the chronology and the limits between innovations. We tried adding spaces, as suggested by this reviewer. However, they were making the figure exceedingly long and more difficult to read.

p18 Figure 4: the unit of measurement of the x axis should be specified clearly (I take it is in 10k years?). Also, for all figures, as a representative for the non-negligible group of males with abnormal color vision, please use color-blind-friendly color palettes and line patterns

*We indicate the units of measurement in the revised figure 4. The colours used in the figures were chosen after numerous trials with the aim of creating the maximum contrast between colours to increase readability and after showing the graphs to several colleagues to make sure they were well readable. Instead of changing colours readability was improved by adding thicked gray lines in figure 3.

Supplementary Materials: would it be too much to ask for a one-liner summary per paper of what the paper shows and why it was included?

*We do not think that adding a one-linear summary per paper would be useful, and this for three reasons: 1) a one-linear summary would not convey to the reader more information than the title of the paper itself, 2) a longer abstract, written with the aim of explaining to cognitive scientists the contribution of each paper to the emergence of the innovation in question, would imply writing 243 short abstracts, 3) in the era of the internet it takes few seconds to a scientist working in a different area to get the full abstract of a paper for free.

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Reviewer #2

The paper defends a view of the evolution of human cognitive abilities where culture plays a leading role. Specifically, it makes two points:

a) the emergence of modern human cultures cannot be causally linked to the emergence and spread out of Africa of H. Sapiens, or to some genetically determined change in H. Sapiens' lineage c. 50 ka.

b) Important cognitive capacities are purely cultural and occur without any genetically determined change. These may include (by order of increasing plausibility): language (or syntax), numeracy, literacy.

These two points are contrasted with a "bottom-up only" view of human cognitive evolution, ascribed to no one in particular but described as prevalent in our field, according to which *all* human cognitive capacities must be genetically determined, with no role played by learning or culture ("only a genetic change my lead to modifications of the brain anatomy and physiology allowing for new cognitive skills required by a novel cultural practice"). In other words, neither learning nor brain plasticity play any role in the emergence of human cognitive capacities.

My first and most obvious objection to this paper is that the "bottom-up only" view that it targets is one of the tallest straw men I ever met (do you know anyone sane who supports it? Please send their names along with a quote and an email address.) This aspect of the paper clearly needs revising.

*The impression that when presenting the “bottom-up only" view we were creating a straw man was coming from a couple of sentences in which we were attributing to colleagues, without mentioning them, the idea that a causal link existed between single cultural innovations and genetic mutations. We have omitted those sentences and rewritten the introduction. In the new text we present the “bottom-up only" view as the shared assumption that a change in the genetic endowment was necessary to the emergence of the package of behavioural innovations that make us different from our phylogenetically closer relatives. Many authors share this assumption and we provide those citations throughout the introduction.

However, a lot of interesting material would remain, I think, once the straw man is out of the way. Point a) — the rise of modern human behaviors wasn't caused by the spread of H. Sapiens — is quite original and well argued. The authors adduce an exhaustive meta-analysis-like dataset concerning the emergence of dozens of distinct technologies all over the globe. This addition will be precious to researchers in many fields and is enough, I think, to justify publication. The cognitive science community will be grateful.

Concerning claim b), I am more sceptical. The author's case is, obviously, very strong for literacy, but then again no one denies that literacy is cultural through and through. (If you know anyone who does, once again, send me their email.) I am not convinced by the claim when it is made about numeracy or language — and above all I am not sure that asking "how much culture? how much genes?" is the right way to ask these questions.

*A body of empirical data supports our claim “B” about numeracy. We already quoted two reviews (Dehaene & Cohen 2007; Nieder & Dehaene 2009) that summarize those data. We have added a new one (Hannagan et al. 2015) in order to strengthen our case. The case of spoken language is indeed more controversial (see answer to next comment).

About language: the authors should either go into more detail here or refrain from raising the topic. There are many distinct components to the human language faculty (phonation; syntax; pragmatics; etc.) — I doubt one can have a meaningful debate without specifying which part of language we're talking about.

*We mention the example of spoken language only indirectly and only to make a general point about our “top-down-also” view. The reviewer is right in saying that the issue of spoken language is a complex one which would require another paper. To address this comment, we now briefly specify that cultural evolution may have affected complex syntax and semantics.

About numeracy, or "arithmetic" as it is called here: Here again it depends how we define it. "Arithmetic" usually means the mathematical manipulation of numbers, but in this paper, it is "the ability to treat exact quantitative information in a symbolic and conventional way". If it is put that way, then it is obviously right (who disagrees?). But the claim that arithmetic is cultural through and through hinges on two words in the definition, "exact" and "conventional". There's a solid case to be made from developmental & comparative psychology for a number sense for exact quantities up to 4. These numbers can be recognised and tracked fluently by babies and by many non-human species. This system's signature limits make it impossible to speak of genuine numeracy, but they also confirm the view that the system is ancient and widespread among animals. A second system can track approximate quantities beyond these small numbers, although it isn't exact.

*It seems to us that this reviewer draws a strong dichotomy between number sense, shared by may animals, and numerical symbols. Our focus is on how did we move from one to another and we argue that the step by step process eventually generating number symbols has been a cultural one and not triggered by a genetic change. We also emphasize that It is exactly the invention of such symbol systems that allows for the treatment of exact quantities much larger than 4. We have slightly changed a number of sentences to better explain this point.

The authors' view on symbolic representations of numbers are original, thought-provoking and backed by a body of justly celebrated first-hand research. Still, I am not

entirely convinced by everything that is said here.
p. 14: I am not convinced that Trinil water shell or Bilzinglehben mammoth bone are indicative of symbolic ascription of meaning to symbols. Same for Les Pradelles bone. Decorative patterns do not necessarily refer to anything: see the nest decorations of Bower birds. The authors could perhaps convince me that these designs are indeed symbolic, but how could we be sure that they are numerical symbols specifically? This seems to be a stretch.

*We do not argue in our text that the Trinil shell or the Bilzingsleben bone carry numerical notations, just that they may have conveyed "iconic, indexical or symbolic" information. The same holds true for Les Pradelles.

The view that numerical graphical symbols were key to the evolution of arithmetic capacities is more debatable than it would seem at first. I defer here to the opinion of Steven Chrisomalis who wrote the book on numerical notations. As he shows, most numerical notation systems evolved as tallies, which don't, strictly speaking, involve the addition or subtraction of full numbers above 1 (a tally only computes 1 +1 +1, etc., occasionally -1). They can also represent numbers, but here again this does not make them fit for arithmetic, as traditionally defined, ie. additions, subtractions, multiplications and divisions of numbers. As Chrisomalis showed, such operations could be performed verbally long before we had practical notations to carry them out graphically. Pythagoras worked with a numerical notation system that was fit for tallying and representing numbers, but lacked proper symbols for the basic operations (let alone more complex ones). Natural language was probably enough to get arithmetic off the ground, as a first step.

*We do not claim that tallies involve arithmetic, rather the opposite. We see tallies and other forms of externalized symbol systems as prerequisite to the development of number symbols and arithmetic.

A more general problem that I encountered while reading this paper was that it seemed to hinge on a simplistic dichotomy between genes and culture. Namely, anything that cannot be accounted for by genes is assumed to be cultural. Yet there is much about human behaviour that depends on learning and plasticity in response to changing environment, without quite involving culture per se. (By culture, here, I mean traditional behaviours passed through long transmission chains that endure across generations.) It is quite possible, for all we know, that the evolution of various human capacities was favoured among other things by new environments and living conditions, without any concomitant genetic change.

*This last observation is a bit surprising because the main point of our paper is precisely to emphasize the role of learning and brain plasticity for the acquisition and transmission of cultural innovations, and promote the idea that these two factors played a prominent role in the evolution of human cognition. In other words our text is in perfect agreement with what this reviewer says here.

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Reviewer #3: Natalie Uomini

This paper is very clear, concisely written, and a broad-ranging review (including new data compiled for this ms) on archaeological and neurological data for cognitive cultural evolution. Epigenetics is here given its rightful place, as it should be. The section 3 treatment of neuroscience is excellent. The text is very well structured. I would suggest only a few minor changes as follows:

on pg. 5, line 11, the list of citations on the debate over a genetic mutation vs. gradual evolution looks like all the sources are supporting a genetic mutation of humans at 50 kya. Bruner or Wynn certainly support a gradualistic view! I suggest to rephrase the sentence to clarify that all of these citations are combined for both sides of the debate.

*We have split the citations between "gradualists" and "mutationists", and added a few to better make the differences between the two stands.

A couple of typos in authors' names appear in the text (Draganski, Roebroeks...), please check them again.

*We have checked this

On Figure 3 and Figure 4, please label the X axes. I assume they are kyr, but it's not clear. Also, my personal preference would be to invert the direction of the X axis so that time is moving forward towards the right, as I feel it's more reader-friendly, but of course that is a stylistic matter.

*We have changed the direction of the X axis of figures 3 and 4.

The data and discussion of Figure 3 are very interesting, a valuable addition to this paper.
Please explain how you chose these categories of "cultural innovations" - perhaps a brief definition of how you define them, so that we may understand e.g. why you do not also include home-bases, long-distance transport of raw materials, or the cultural use of bird feathers. Also, please specify which hominin species are included in this dataset.

*We better explain how we choose the innovations, provide a definition of “cultural innovation” for the purpose of our paper, and specify as much as possible the hominin species included.

The list for control of fire is lacking all citations by J. Gowlett, who has arguably the most important data (Beeches Pit, Chesowanja.....), as well as latest fire results by N. Goren-Inbar (I am not sure if all of these are within your time frame of 850 kya, but it might be worth expanding the window to include these). For hafting, I would also check L. Barham's new book on this topic.

*We have added a reference to Gowlett and a new article on this topic by Sangathe. Two papers by N. Goren-Ingar are already in the list of references. We have also added L. Barham book in the references

On page 14 you mention Bilzingsleben, but I would cite that with caution, given all the works by C. Pasda and colleagues showing that the site was mostly natural and that nearly all of the supposed cultural artifacts were not human-made.
*We have added this reference. However, this study does not demonstrate that the site is natural, just that there is a previously undetected natural component in it.

Overall the ms is a joy to read!

Culture: the driving force of human cognition

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Keywords: Palaeolithic, behavioural modernity, cultural evolution, exaptation, neural reuse, gene-culture co-evolution, neuroplasticity, cultural innovations.

1. Introduction

As far as the evolution of cognition is concerned, the key challenge nowadays is to ascertain the relationships among four levels of involved factors: the genetic endowment, the brain anatomy and physiology, the cognitive skills, and the cultural practices. A shared view is that a species' genetic endowment sets the species-specific brain gross functional anatomy and normal physiology, which enables the array of cognitive skills available to the individuals of a certain species, which in turn determine the "typical" behavioural patterns expressed by individuals and populations of that species (Tinberg, 1951; Shettleworth, 2010; Miklosi, 2014; Herculano-Houzel, 2017; Santolin & Saffran, 2017; Moss, 2018).

Crucially, as far as humans are concerned, those behavioural patterns include the "key cultural innovations" – i.e. innovations that are so momentous that they spawn an array of secondary products or behaviours (Reader & Laland, 2003) – that make us different from our phylogenetically closer relatives (e.g., making composite tools, creating symbolic items, developing literacy and numerical symbol systems, or even speaking an articulate language). Such novel cultural practices deeply affect cognition and are underpinned by dedicated brain networks. Therefore, such a view implies a strong "chain of dependence" from genes, to brains, to cognitive skills, to some key adaptations shared by all human cultures (Fig. 1) (for recent reviews, see: Geschwind & Rakic, 2013; Somel et al., 2013). Let us call this view the "bottom-up-only" view. Importantly, a corollary of this view is that for these typically human behaviours to emerge, a change in the genetic endowment was ultimately and necessarily required. Indeed, according to the "bottom-up-only" view, only a genetic change my lead to modifications of the brain anatomy and physiology allowing for new cognitive skills required for the development of the package of innovations that made us humans.

The challenge, therefore, is to establish whether genetic changes are the cause or the effect of the novel cultural practices (especially as far as relatively recent periods and relatively short time-spans are concerned). According to the "bottom-up-only" view, the answer would be that the related genetic changes are the cause of – or, at least, the necessary condition for – the emergence of the (key) cultural novelties. We will see in the following how and why this is not the only, and perhaps not even the best, possible answer. Before introducing an alternative scenario, let us add a few specifications about the "bottom-up-only" view.

-----------------------------Insert Figure 1 about here ------------------------------

First, according to the “bottom-up-only” view, the genetic changes necessary for the cultural novelties to emerge does not need to occur “immediately before” the latter. There may be time-lapses between the two, even considerably long. However, the genetic changes should be causally related (as a cause to its effect) to the emergence of the cultural novelties – i.e., without that genetic change no such and such cultural novelties might have been produced. With this specification in place, the “bottom-up-only” view can account for cultural novelties deriving from genetic changes not only as “adaptations” but also as (biological) “exaptations” (Gould & Vrba, 1982; Gould & Lewontin, 1979), and even as the outcome of enduring “directional selection” (Price et al., 1988). In all these cases, indeed, underling and causally related genetic evolution is involved (see also Colagè & D’Ambrosio, 2014).

Second, the “bottom-up-only” view does not imply that the genetic changes responsible for the emergence of key cultural innovations be of such a large an extent to determine speciation events. In other words, genetic changes leading to key cultural innovations may well occur at the micro-evolutionary level (i.e., roughly, *“within”* the evolution of a given species), and not only – as it is obviously the case – at the macro-evolutionary level (i.e., at the level of evolution of new biological species). In this sense, the “bottom-up-only” view encompasses all those proposals according to which the earliest appearance of “cumulative culture” – defined as the ability of a culture to accumulate and improve innovations over time – would have been the outcome of either the speciation event leading to *H. sapiens* in Africa ca 260 ka (McBrearty & Brooks, 2000; Mithen, 2005; Coolidge & Wynn, 2004, 2007, 2017, 2018; Wynn et al., 2016; Shea, 2011; Bruner, 2014; Bolhuis et al., 2014; Neubauer et al., 2018) or of a key genetic change occurring ca 50 ka and inducing a switch in the neural constitution of *H. sapiens* (e.g., Mellars & Stringer, 1989; Klein, 1989, 2000; Tattersall, 1995; Bar-Yosef, 1998).

A number of empirical findings and theoretical advancements of the last few decades make the sketched “bottom-up-only” view less and less plausible. The aim of this paper is to envisage a novel mechanism for cognitive evolution in which culture is the driving force, thus offering what we call a “top-down-also” view of human cultural evolution. The idea behind this mechanism is that cultural innovations have direct effects on the cognitive capabilities of populations of hominins (via what we call “cultural exaptation”) and on the neural substrates of individuals (via what we call “cultural neural reuse”).

Four topics are relevant to introduce this mechanism. The first topic is epigenesis and phenotypic plasticity (Jablonka & Lamb, 2005; see also D’Ambrosio & Colagè, 2017). This research line, broadly speaking, highlights that the phenotype should not be considered as the mechanistic outcome of a genotype. Consequently, phenotypic variation – i.e., the "transmutation of forms" (Pigliucci, 2009) – is not generally due *only* to genotypic variation. Novel phenotypic configurations can be induced by environmental factors without implying any change in the DNA nucleotide sequence. One of the most striking examples of this is provided by the marked morphological and behavioral differences of *genetically identical* working versus queen honey bees (*A. mellifera*), that are due to specialized diet during development (Lyco et al., 2010). Another example is the so-called ''masticatory-functional hypothesis'' for craniofacial changes (Corruccini, 1984; Varrela, 1992, 2006; Tang et al., 2004), according to which decrease in jaw dimension and increase in occlusal variation displayed by modern humans do not depend on genetic alterations but on the transition from pre-industrialized food to modern soft diet, which requires less chewing force and time. This overall perspective also implies that phenotypic evolution does not coincide with, or follow the same rate as, genetic evolution. Now, once "phenotype" is understood as encompassing cognition and behavior besides morphology, anatomy and physiology, and once "environment" is understood as including cultural practices, the relevance of epigenesis and phenotypic plasticity for "the cultural evolution of cognition" appears clearly.

The second topic, directly related to the previous one, is neuroplasticity (or brain plasticity). Neuroplasticity indicates the ability of the brain to modify physiological, functional and/or structural features as a consequence of experience and practice, or following brain lesions, virtually all along the individual lifespan, though at different degrees in different periods (Pascual-Leone et al., 2005; Johnson, 2001, 2011). The human brain is peculiarly plastic, and measurable brain changes (at both grey- and white-matter level) can be detected even after relatively brief periods of practice in novel tasks (e.g., Draganski & May, 2008; Hecht et al., 2014). We will come back to this topic in Sect. 3. It is however clear that neuroplasticity opens the possibility for novel "brain phenotypes" (potentially able to support new cognitive skills and cultural practices) to be produced and – most importantly – *stabilized* in a population without requiring concomitant genetic changes.

The third topic to be addressed is so-called gene-culture co-evolution (e.g., Laland et al., 2010; Gintis, 2011; Richerson et al., 2010; Varki et al., 2008). In the last forty years, starting from the path-breaking work by Feldman and Cavalli-Sforza (1976) on adult lactose tolerance in human populations with a history of dairy farming, a number of cases have been enquired (by both empirical work and mathematical modelling) in which the existence of a specific cultural practice in a population directly affects the genetic evolution (allele distribution) of individuals within that

population. Though gene-culture co-evolution mainly involves, at the genetic level, "classical" mechanisms of population genetics, the relevant point is that the concerned cultural practices (and the related cognitive skills) emerge and (begin to) stabilize *before* genetic evolution takes place.
Finally, as for the fourth topic, it is worth stressing that a number of recent proposals from different disciplines suggest – or, at least, allude to – the idea that some key innovations in human history and prehistory may have been essentially due to "culturally driven evolution" (Heyes 2012, 2018; Dor & Jablonka, 2014; Laland, 2017), or to truly cultural evolution with "little if any" strictly biological (namely, genetic) evolution. Interestingly, the latter idea is often applied to one of the most peculiarly human cognitive, cultural and symbolic ability: spoken, articulate and highly-syntactical language. The consequences of articulate language on human cognition are enormous, for sociality, communication, conceptual thinking, material culture (mainly via teaching), theoretical culture, personal and social identity, etc. It is also clear that articulate language is the outcome of a long evolutionary process leading to a brain complex enough to support it, and that such process involved a wealth of genetic evolution (e.g., Maricic et al., 2013; Fisher, 2017). In spite of this, some authors suggest that at least the most recent stages of language evolution (mainly concerning complex syntax and semantics) are *culturally*, and not biologically driven (Evans & Levinson, 2009; Dor & Jablonka, 2014; Bickerton, 2014; Anderson, 2014; Arbib 2013, 2016; see also Colagè, 2016).

------------------------------Insert Figure 2 about here -------------------------------

All this prompts what we would call a "top-down-also" view for the evolution of cognition. Such a view claims, broadly speaking, that cognitive evolution is not driven exclusively by genetic evolution, not even as far as key cultural innovations are concerned. On the contrary, the "top-down-also" view maintains that truly cultural evolution *can* trigger the emergence of new cognitive skills also independently of any heritable change in the genetic make-up of organisms (Fig.2a). In other words, the idea is that cultural and cognitive novelty may emerge and stabilize even without any concomitant change at the genetic level. This view seems to be compatible with the mentioned advances in epigenesis and phenotypic plasticity, especially as far as the phenotype is understood as encompassing also cognition and behavior besides morphology, anatomy and physiology. It will also elaborate on the suggestion that especially the recent stages of the evolution of genus *Homo* and *H. sapiens* are mainly culturally driven. Moreover, the "top-down-also" view may add a new implication to the issue of gene-culture co-evolution. It is part and parcel of gene-culture co-evolutionary approaches that culture is the leading factor and that genetic evolution "just" follows. However, there might be cases in which the ensuing genetic evolution is *inessential* not only to the emergence of a key cultural innovation, but also to its spread and stabilization within and across populations. As we will see (Sect. 3), indeed, there are data suggesting that the emergence of cultural novelties via genuinely cultural evolution not only may affect cognitive skills, but also the underlying neural substrates without requiring genetic evolution, and that the novel cultural process, related cognitive skills and underpinning neural substrates may spread and stabilize much before any "genetic accommodation" to those novelties appears (Fig. 2b).

In the following, we will first summarize (Sub-sect. 2.1) a number of archaeological data seemingly incompatible with the "bottom-up-only" view and in line with the "top-down-also" view. Then, we will propose a mechanism for cultural evolution – what we call "cultural exaptation" – able to offer an understanding of how cultural evolution may proceed without the need for underlying genetic evolution. After that, in Sec. 3, we will report data showing how cultural innovations have the potential to induce measurable changes in the brain that are (i) crucial for the stabilization of those innovations, and (ii) independent of any concomitant and causally-related genetic change. All this will delineate a promising and operative understanding of how culture may actually be "the driving force of human cognition".

2. From Culture to Cognition

2.1 Patterns of Cultural Innovations

To the aim of supporting the "top-down-also" view for the evolution of cognition from the archaeological standpoint, Fig. 3 shows the temporal and geographical pattern of cultural innovations in the last 800 ka. By cultural innovations we mean, in this context, typically human behavioral traits leaving detectable traces in the archaeological record. Fig. 3 synthesizes what is currently known about the emergence of these traits, and stems from a review of the literature relative to the occurrence of twenty-nine cultural innovations in four geographical areas: Africa, Near East, Europe, Asia. Its primary purpose is to highlight differences in the timings and pace of innovations' emergence and to explore whether a correspondence exists between particular fossil species and specific arrays of cultural innovations. The innovations concern subsistence-strategies, technology and symbolic behavior. We have selected innovations with obvious consequences on cultural complexity and discarded those based on circumstantial evidence, i.e. evidence that relies on an inference to connect it to a conclusion. Recent innovations, such a pottery, domestication, and writing were not considered. Literature mining was based on previous compilations (McBrearty & Brooks, 2000; d'Errico, 2003; Villa & Roebroeks, 2014) and recent discoveries concerning each innovation category (see Supplementary Material). The choice of the regions, admittedly different in size, was conditioned by previous compilations, different data availability and, to some extent, the chronology of modern human expansion, with Africa and subsequently the Near East representing the first two regions recording such expansion. Although the emergence, adoption, loss or reinvention of most innovations cannot be connected with certainty to a particular fossil hominin, different fossil populations lived during the considered time span, including *Homo erectus, Homo antecessor, Homo neanderthalensis, Homo heidelbergensis, Homo sapiens,* and probably other populations of the genus *Homo* such as the Denisovians.

-----------------------------Insert Figure 3 about here ------------------------------

Eight main considerations emerge from the analysis of the graphic representation of the data and a critical analysis of the literature:

1) Isolated occurrences of key innovations (shell-fishing, microliths), including possible instances of symbolic material culture (abstract engravings, carvings) are reported at very ancient sites (800-300 ka) from the four regions.
2) A number of long-lasting innovations linked to subsistence (control of fire, hafting, blade production, grindstones use) but also to possible symbolic activities (some mortuary practices, ochre use) are attested in Africa, Europe, the Near East and, to a lesser extent, Asia, between 500 and 250 ka.
3) An array of innovations (i.e. formal bone tools, pyrotechnology, use of mastics, marine and fresh-water fishing, personal ornaments, engravings, objects coloring) appears in Africa between 100 and 70 ka. However, these innovations are almost exclusively found at few sites in Northern and Southern Africa, disappear in some cases for 5-10 ky to reappear again in different forms. Many are found in Europe and the Near East before the arrival of modern humans in these two regions.
4) Other innovations (rock art, possible systems of notations, use of poison) appear permanently everywhere only from 50-40 ka or later, with possible precursors in Europe 64 ka.

5) Most innovations recorded in Africa, Europe and the Near East before 50 ka are found in Asia only after that date.
6) A number of isolated instances reported in the literature would require a critical reassessment before being accepted.
7) In a number of cases, future discoveries may fill in the gap between early isolated and more recent consolidated occurrences.
8) Since early occurrences of a number of key innovations were unknown a decade ago, we may expect that future archaeological discoveries will almost certainly identify earlier occurrences of some innovations.

While keeping the last three caveats in mind, the above points suggest that the timing, location, and pace of innovations' appearance is inconsistent with scenarios attributing the spread of modern cultural traits to concomitant genetic evolutionary processes. No concomitant raise of innovations that one might associate to a sudden shift in human cognition produced by genetic change or speciation is observed at any given moment in the past, in a particular region or population. No accretion of innovations is exclusively observed in only one single region. Many subsistence-related cultural achievements previously considered as the exclusive legacy of modern humans also occur among anatomically "archaic" populations such as Neanderthals. Complex and changing technologies – including the ability to produce blades, use of grindstones and mastic, heat treatment of rocks, hafting techniques, varied strategies to hunt dangerous games, exploitation of marine and plant resources, ability to ignite and control fire, organization of living space, sea fearing – are among the innovations that are now recognized as inherent to Neanderthal cultures in Europe, and this before any contact with modern humans (d'Errico, 2003; d'Errico & Stringer, 2011; Villa & Roebrokes, 2014). Several lines of evidence support the view that symbolically mediated behavior also played a role in Neanderthal cultures. Treatment of the body after death, collection of rare natural items, engraved and perforated objects, personal ornaments, pigment use, extraction of bird feathers and claws probably for personal decoration, and abstract patterns engraved on cave walls are among the significant symbolic achievements now firmly attributed to Neanderthals. The virtual absence or discontinuous occurrence of such cultural innovations in Asia before anatomically modern populations colonized this region does not necessarily reflect, in the light of what we have seen so far, built-in cognitive differences, but could be explained by rather different cultural trajectories less relying on cultural transmission and accumulation of knowledge or, alternatively, to lack of research in, and data coming from, large regions of this continent.

Therefore, cultural innovations seem to appear, disappear and reappear (with different specifics) at different times, in different places, and among different human fossil species across the four geographical areas considered. Such complex patterns of cultural innovation seem utterly incompatible with a scenario in which key cultural innovations would need concomitant and/or directly causally-related genetic changes. Consequently, the overall trajectory (Fig. 4) of cultural innovations in recent human evolution seems incompatible with the "bottom-up-only" view, and arguably supports the idea that cultural dynamics may be the leading force of cognitive and cultural evolution, consistently with the "top-down-also" view sketched above (Sect. 1).

-----------------------------Insert Figure 4 about here ------------------------------

2.2 Cultural Exaptation: How Culture Affects Cognition

Here, we propose a plausible mechanism potentially able to explain the progression in cultural evolution. The notion of exaptation was introduced by Gould and Vrba (1982) in the field of evolutionary biology to indicate traits that have not been selected for their current function, but that evolved either for another function or for no specific function (see also Gould & Lewontin, 1979). A classical example of exaptation is that of birds' feathers (Gould & Vrba, 1982), which apparently first emerged for thermoregulation and were only later "exapted" for flying, and successively refined and diversified for the various flying needs of their carriers.

Cultural exaptation refers to the co-option of existing cultural features for new purposes. Cultural exaptation, as understood here, does *not* require concomitant biological exaptation or *heritable* genetic changes as a prerequisite, but occur at the truly cultural level. In analogy with biological exaptation, however, the co-opted cultural feature was originally devised for purposes quite different from those for which it later became "culturally exapted".

The use of ochre (pigment containing hydrated iron oxides) may provide an example. It has been shown that compounds made with ochre offer effective photo-protection shielding the skin from harmful ultraviolet radiation (Rifkin et al., 2015). There is evidence suggesting symbolic use of iron-rich pigments on personal ornaments since at least 80 ka in Africa (d'Errico et al., 2009; d'Errico & Blackwell, 2016). One can envision a scenario in which ochre was first exploited for its photo-protective function and, in a later phase, culturally exapted – e.g. in body painting – to reinforce cultural mechanisms related to intra- and inter-group self-identification spurring the emergence of diversified symbolic material cultures. A subsequent cultural exaptation may have occurred in an already fully symbolic context, when ochre was purposely employed on ornaments and clothes.

Another key example is provided by incised objects progressively acquiring more and more conventional symbolic meanings up to formal Artificial Memory Systems (AMSs) – defined as devices specifically conceived to store and recover information (e.g. d'Errico, 1998, 2002) – and the final development of number symbols (d'Errico et al., 2017). We have proposed that the invention of number symbols required at least five, not necessarily successive, stages or cultural exaptations. The first, "baseline" stage consists in the motor and cognitive skills necessary to produce durable and visible markings on bones with stone tools, an ability highly likely related to butchery activities as old as 2.6 Myr (Domìnguez-Rodrigo et al., 2005, 2016). From this, a first cultural exaptation may have occurred when visible incised patterns, composed of cut-mark-like lines, were purposely produced on bone or other materials to give rise to detectable abstract designs with iconic, indexical or symbolic functions. Engraved fresh-water shell from Trinil (Joordens et al., 2015) and the pattern engraved on the Bilzingsleben mammoth bone (Mania & Mania, 1988, but see Müller & Pasda, 2011) indicate that this practice may have been already in use at least 540 ka BP. A following exaptation, exemplified by the pattern engraved on the Les Pradelles bone (d'Errico et al., 2017), may have occurred when meaning was attributed to identical individual marks (rather than to the whole pattern) produced during the same session. This type of AMS was possibly in use already 60 ka, and probably earlier (d'Errico et al., 2017). A third exaptation occurred when similar marks were incised at different times, which gives the possibility of adding numerical information to an already existing pattern. The Border Cave notched bone (d'Errico et al., 2012; d'Errico et al., 2017), dated to 44-42 ka BP, is the earliest known example of such a notation type. A fourth exaptation occurred when the morphology of the marks, their spatial distribution, their number and their accumulation over time were individually or conjointly given a role in the code. The earliest known examples of such devices date back to 40-38 ka (d'Errico et al., 2012, 2017). This fourth exaptation contains most of the premises that did eventually allow some human populations to produce a further exaptation: the invention of the number symbols and numerical notations known historically and used at present. The invention of symbolic number systems (and of arithmetic) clearly had enormous consequences on human cognition and life-style more generally. This is manly due to the fact that a symbolic and conventional system allows for processing exceedingly large quantities.

Cultural exaptation, as exemplified here, has the potential to provide a mechanism for truly cultural evolution, and *ensuing* cognitive evolution – i.e., a mechanism according to which (i) culture is a cause (sometimes, the primary or even the only cause) of human cognitive evolution and, (ii) human cognitive evolution does not need concomitant genetic evolution as its necessary cause.

The concept of cultural exaptation differs from that of cumulative culture in that, consistently with its biological counterpart, it refers to the use of an existing cultural trait for a new purpose while cumulative culture may proceed via refinement of solutions having the same function. A supplementary difference lies in that cultural exaptation is deliberately disjoint from taxonomic affiliation while many authors consider the ratchet effect associated with cumulative culture as a characteristic feature of our species (Tomasello 2009; Tennie et al., 2009). Moreover, cultural exaptation is fully compatible with losses of cultural innovations and is not inevitably cumulative.

3. From Culture to the Brain: Stabilizing Key Cultural Innovations

So far, we have proposed how culture – via what we have called "cultural exaptation" – may be seen as the driving force of human cognitive evolution (Fig. 2a). However, emergence of cognitive skills requires adequate brain substrates – i.e. brain circuits, systems or networks able to support the cognitive functions implicated in novel cultural practices. According to the "bottom-up-only" view (Sect. 1; Fig. 1) new brain systems may emerge, fundamentally, only as a consequence of biological (namely, genetic) evolution. Indeed, formation of new brain networks able to support novel cognitive skills and cultural practices is usually assumed to require changes at the level of the species-specific genetic-epigenetic program mastering the development of the brain gross functional anatomy (which indeed specifies the distribution of different kinds of nerve cells in the brain, and the patterns of anatomical connectivity linking distinct brain areas). We have already seen (Sect. 1) that some recent advancements about so-called developmental neuroplasticity indicate that brain development and maturation is significantly affected by environmental factors (also including social and cultural dimensions) and the individual's detailed life history. This suggests, at the general level, that many aspects of brain anatomy, physiology and functionality do not mechanistically follow solely from the available genetic endowment. Of course, the peculiarly high brain plasticity of human beings is the outcome of a long biological and genetic evolutionary path (Somel et al., 2009; Charrier et al., 2012); brain plasticity has probably been selected for (likely mainly via directional selection) along evolution. Moreover, the idea that experience may fine tune brain circuits and networks does not necessarily debunk the "bottom-up-only" view. Brain circuits may be refined by experience the same way as the muscular-skeletal, the digestive and/or the circulatory systems are forged by individual life history. This, by itself, does not exclude that the basic outlook of those systems is genetically specified.

However, there is increasing evidence that the formation of *new* brain networks (i.e. brain networks not generally foreseen by the species-specific brain gross functional anatomy) may be induced by cultural practices without the need of any concomitant or directly causally-related changes in the heritable genetic-epigenetic endowment of individuals. Interestingly, one such cultural practice is arithmetic (the ability to treat exact quantitative information in a symbolic and conventional way) – that we already considered in the previous section. Another key case is that of literacy (the invention of writing systems, i.e. systems able to translate an existing articulate language in *visual* symbols). We cannot enter into too much details here. However, the idea of "cultural recycling of cortical maps" (Dehaene & Cohen, 2007; Hannagan et al., 2015) has been proposed to account for the invention of these two recent cultural innovations. The idea is that once an individual learns such cultural practices, existing brain areas, emerged in our evolutionary past *for other purposes*, are reused (recycled, co-opted, etc.) to support those new practices. There is consistent evidence that both literacy and arithmetic recycle existing brain tissue evolved (a) in the fusiform gyrus for processing faces and high-resolution sharp-edged visual shapes in the case of literacy (Dehaene et al., 2015), and (b) in the intra-parietal sulcus for rough estimation of amounts of stuff in the case of arithmetic (Nieder & Dehaene, 2009). Two points are to be stressed. First, both literacy and arithmetic are too recent inventions – and have spread too fast across virtually every human population on Earth – to be direct outcomes of genetic evolution. Second, it seems that recycling existing brain tissue for the novel cultural practices also involve non-local, inter-regional re-arrangement of entire brain networks. As to this second point, data are clearer about literacy. It may indeed be suggested that acquiring literacy requires not just the refinement of *existing* anatomical networks, but the actual *formation of a new*, anatomically implemented brain network specifically dedicated to reading. In particular, there is evidence that acquiring literacy not only requires the formation of a new *functional* network putting the left fusiform face area (FFA) at the service of literacy (Caspers et al., 2013, 2014), but also the strengthening of the anatomical connections of the mid-fusiform gyrus with other perisylvian regions (like, superior-middle temporal and inferior parietal areas) involved in spoken language (Thiebaut-de-Schotten et al., 2014; Yeatman et al., 2012; Klingberg et al., 2000). Acquisition of literacy would thus be a case in which a novel cultural practice not only prompts new cognitive skills, but also directly and significantly affects brain organization at the level of formation of new anatomical networks (Fig. 2b).

In analogy with our notion of "cultural exaptation" (Sub-sect. 2.2), we propose to label the just-mentioned kind of consequences that culture may have on brain substrates as "cultural neural reuse". Cultural neural reuse might provide a further mechanism, this time at the neural level, thanks to which newly emerging cultural practices (via cultural exaptation) may be *stabilized* within and across human populations by specifying dedicated brain networks without the need for genetic evolution. Thus, cultural neural reuse contributes to argue for culture as the driving force of recent human evolution at both the cognitive and the neural level (Fig. 2b).

4. Conclusion

We began by contrasting two basic approaches to the evolution of cognition: the "bottom-up-only" view and the "top-down-also" view (Sect. 1, Figs. 1 and 2). We have also tried to show how the first view seems less and less compatible with a number of advancements in the life-sciences, and that these advancements encourage the adoption of the second view. Then, in Sect. 2, we have offered arguments in favor of the "top-down-also" view coming from archaeology. We first proposed that the pattern of cultural innovations of the last 800 ky, as attested in the archaeological record, is arguably incompatible with the idea that for any key cultural innovation to emerge, concomitant and directly causally-related genetic evolution is required (Sub-sect. 2.1). After that, we have proposed a possible and general mechanism (cultural exaptation) potentially able to account for how key cultural innovations may emerge according to genuinely cultural processes and without requiring concomitant genetic evolution (Sub-sect. 2.2). Finally, we have briefly discussed (Sect. 3) recent advancements in the neural sciences presenting cases in which cultural practices may induce the formation of novel brain networks – anatomically (and not only functionally) implemented – again without implying genetic evolution (cultural neural reuse).

The combination of cultural exaptation and cultural neural reuse may provide an overall mechanism through which culture may have become the leading force of human recent cognitive and neural evolution. This would be the essence of what we have labelled as the "top-down-also" view. In a nutshell, we argue that successive cycles of cultural exaptation and ensuing cultural neural reuse represent the fundamental mechanism that has regulated the cultural evolution of our lineage. This mechanism accounts for the asynchronous and patchy emergence of innovations around the globe. It also serves as a satisfactory explanation for trends toward complexification of cultural practices recorded at different times and places in human history. It is theoretically not impossible that on longer time-scales, the innovations stabilized through the proposed mechanism become somehow “genetically assimilated” (Waddington 1942, 1953; see also Varki et al. 2008), and this may well happen via gene-culture co-evolution. However, this would be a subsequent stage that is not strictly required for significant cultural innovations to become stabilized, spread and transmitted from generation to generation.

Therefore, our proposal is not aimed at suggesting that genetic evolution is irrelevant to human cognitive and/or cultural evolution. Both cultural exaptation and cultural neural reuse always build upon pre-existing cultural practices, cognitive skills and related neural substrates that generally are the outcome of previous biological and genetic evolution *stricto sensu*. The review of the archaeological data suggests that biological setting on which cultural exaptation and cultural neural reuse acted to promote cultural evolution are a characteristic of our genus rather than of our species.

However, our proposal suggests that culture should be regarded as an effective causal factor in human evolution, not only in the sense that cultural environments exert specific selective pressures on organisms, but also as a source of novelty independent of genetic changes and natural selection. It is compatible with the idea that cultural evolution may affect genetic evolution (via gene-culture co-evolution), but also suggests that cultural innovations may stabilize before (or even without) corresponding genetic changes, so that the accelerating pace of human genetic evolution (Hawks et al., 2007; Evans et al., 2005) may be an *inessential* consequence of cultural evolution, at least in some relevant cases.

Moreover, our proposal might be helpful in letting scholars from various disciplines (genetics, evolutionary anthropology, cognitive sciences, neural sciences, archaeology, etc.) cooperate in view of an encompassing and interdisciplinary understanding of human culture and cognition that takes into account the real complexity of the involved factors.

Finally, we think that the “top-down-also” view sketched here – articulated in terms of cultural exaptation and cultural neural reuse – not only is in line with recent advances in the life sciences (as discussed in Sect. 1), but also builds upon them in a constructive way.

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Figures Legends

Fig. 1. Schematic representation of the “bottom-up-only” view.

Fig. 2. Schematic representation of the “top-down-also” view. a) Culture may directly affect cognition via “cultural exaptation”, thus triggering the emergence of new cognitive skills without requiring concomitant genetic changes. b) Culture may directly affect also brain anatomy via “cultural neural reuse”, thus favouring the emergence of novel brain network without requiring concomitant genetic changes.

Fig. 3. Occurrence of cultural innovations in four regions of the world during the last 850 ky. (See Supplementary Material)

Fig. 4. Frequency of cultural innovations in the last 850 thousand years at the regional scale and (insert) at the global scale. This graphs summarize the data shown in Fig. 3.

Dear Fiona,

Thank you for the opportunity to resubmit a revised version of our manuscript *Culture: the driving force of human cognition*. We address below, introduced by an asterisk (*), on a point by point basis, how we have addressed the comments raised by you and the reviewers. As you will see, we have made almost all the changes suggested by you and them, including those concerning the figures. We think that, thanks to the comments and issues raised by the reviewers and synthetized by you, the paper is now much stronger. We hope that the revised manuscript will be accepted by TopiCS as we believe that it is a significant contribution and of interest for a large scientific audience.

We look forward to hearing from you

With kind regards,

Ivan Colagé and Francesco d'Errico

P.S.: Please, notice the Ivan Colagè is the first and corresponding author of this article. It appears as the second author in the submission system since the manuscript was submitted by Francesco d'Errico and the system did not allow to indicate a different first and corresponding author. The order of the authors is correctly indicated in the revised manuscript. Thanks.

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Editor

R1 and R3 are especially enthusiastic and make only minor points. R1's comments regard your stance on various literature; give suggestions to improve the figure; and have a request regarding the SM. The last point (to give a one line summary of each paper) would turn this bibliography into an exceptionally useful resource. My sense is that your Figure 3 is so usefully summative and beautiful that the effort required on the bibliography would be well worth it. I urge you to take this suggestion on. I agree with R3 on the orientation of the Figure, given that in a majority of literate traditions, time moves from left to right.

*See below the changes made to address these concerns

R2 makes astute observations on your characterisation of the bottom-up and top-down views. I concur that the extreme bottom-up view is difficult to pinpoint on particular scholars (you point the reader to reviews that do not seem to speak to human evolution directly), but if the dichotomy is to remain, then you must address this point. One potential solution would be to re-envision your contrast as a continuum. Whichever you choose, please address R2 on this. R2 also remarks on each of the individual cognitive capacities that you present evidence for, and has useful suggestions for strengthening your case. Please implement and/or consider these accordingly in a response.

*See below the changes made to address these concerns

Along with R2, my sense is that the top-down perspective is not as well-characterised as it could be either. R2's opinion is that your genes-culture dichotomy is simplistic, but I think it is simply that there is nuance in your in-between stages to bring out in revision. Editorially, I do think that more explanation of HOW the cultural evolution of cognition works is needed.

*We have added two paragraphs in the Conclusion section in which we explain how we think cultural evolution may work according to the “top-down-also” view, and problematize relationships between genes and culture so to make our dichotomy appearing less simplistic. We also explain that the biological foundation upon which cultural evolution builds up are, according to our review of the archaeological evidence, a characteristic of our genus rather than our species.

In the section beginning “Finally, as for the fourth topic“ on culturally-driven evolution, there is a notable omission of the perspectives of Cecilia Heyes. Ideas in her 2012 “Grist and Mills” in Phil Trans Roy Soc, for example, or her recent book Cognitive Gadgets. Similar ideas regarding the cultural evolution of language are apparent in Evans and Levinson 2009 BBS.

*We have added these references. Thank you pointing them to us.

Finally, I have some small comments of my own.

Introduction
The aim of the paper is in the abstract, but it also needs to be stated in the intro earlier (p4 15-17 “A number of empirical findings …”).

*We now state the aim of the paper after this sentence

Section 2.1
Figure 3 is a lovely rich visualisation from which many important inferences can be drawn. While references are listed in the supplementary material, please help the reader a little more. In the text justify why the data are presented by region / give earliest evidence for human occupation / state that a number of species are considered here etc.

*We better explain the purpose of the figure, why the data are presented by region, and the number of fossil species considered (a request also made by reviewer #3).

Moreover, lines 52-56 on p.11 are key to understanding this section. For the cognitive science audience, present this information earlier in section 2.1 to show what the purpose of the figure will be. Similarly, lines 35-39 on page 12 will help the reader interpret the figure and can come at the beginning of this paragraph.

*We added a sentence at the beginning of section 2.1 in which we clarify the purpose of the figure and what kind of inferences can be made from it..

Each of the points 1-5 is explained further in text, but perhaps this whole section could be reworked so that the “consideration” is followed immediately by the implications on page 12.

*We have tried to follow this suggestion but ended up with a text that appeared to us less incisive than that of the submitted manuscript.

2.2 Exaptation
Is there an opportunity to either link more closely, OR, demarcate more clearly, your notion of cultural exaptation and that of cumulative cultural evolution?

*We have explained the difference between cultural exaptation and cumulative cultural evolution at the end of section 2.2

If any remarks are not clear, I am happy to clarify and advise further. When resubmitting your revision, please indicate in an accompanying letter how you addressed the various points raised by the reviewers.

Best wishes
Fiona

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Reviewer #1: Dan Dediu

There is very little I do *not* agree with in the paper (maybe this makes me too lenient a reviewer?), and I would argue that indeed most of these ideas are becoming the new "common ground" when thinking about human evolution (not in small part due to the authors' own primary research and theorizing!): this is why I had to go for only a "3" on originality. Nevertheless, I think that it is precisely such papers that help popularize these views outside the specialist community and improve their fit to the empirical data, so I would strongly urge its publication.

I do, however, have some small comments:

p4, 9-12: I don't think that the ASPM/MCHP1 2005 papers are taken seriously in the genetics literature anymore, especially in what concerns their claims about "recent and ongoing" adaptive evolution -- the methodology used (coalescent simulations) is quite open to criticisms and later work seems to convincingly show that while the "old" selective pressures and the geographic patterning are probably real, the "recent and ongoing" ones are probably due to population structure

*We have eliminated the paragraph in question

p4, 14-22: the evolutionary story of FOXP2 is is much more complex that described here, and the authors seem to have missed (or decided not to mention) all the juicy stuff that came out of Svante's lab post 2002 including refining the selective signal on FOXP2 (actually, there might have been at least 2?) and when & why it might have happened...

*We have eliminated the paragraph in question as a detailed review of the FOXP2 is outside the scope of our article p5 23: probably "mechanistic"?

*Corrected

p10 Figure 3: I think the figure might become easier to follow if: (a) there would be some space separating the 4 rows of each innovation, and (b) vertical guides at say each 100k

*We have added vertical and horizontal lines in a darker gray. They help the reader to better identify the chronology and the limits between innovations. We tried adding spaces, as suggested by this reviewer. However, they were making the figure exceedingly long and more difficult to read.

p18 Figure 4: the unit of measurement of the x axis should be specified clearly (I take it is in 10k years?). Also, for all figures, as a representative for the non-negligible group of males with abnormal color vision, please use color-blind-friendly color palettes and line patterns

*We indicate the units of measurement in the revised figure 4. The colours used in the figures were chosen after numerous trials with the aim of creating the maximum contrast between colours to increase readability and after showing the graphs to several colleagues to make sure they were well readable. Instead of changing colours readability was improved by adding thicked gray lines in figure 3.

Supplementary Materials: would it be too much to ask for a one-liner summary per paper of what the paper shows and why it was included?

*We do not think that adding a one-linear summary per paper would be useful, and this for three reasons: 1) a one-linear summary would not convey to the reader more information than the title of the paper itself, 2) a longer abstract, written with the aim of explaining to cognitive scientists the contribution of each paper to the emergence of the innovation in question, would imply writing 243 short abstracts, 3) in the era of the internet it takes few seconds to a scientist working in a different area to get the full abstract of a paper for free.

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Reviewer #2

The paper defends a view of the evolution of human cognitive abilities where culture plays a leading role. Specifically, it makes two points:

a) the emergence of modern human cultures cannot be causally linked to the emergence and spread out of Africa of H. Sapiens, or to some genetically determined change in H. Sapiens' lineage c. 50 ka.

b) Important cognitive capacities are purely cultural and occur without any genetically determined change. These may include (by order of increasing plausibility): language (or syntax), numeracy, literacy.

These two points are contrasted with a "bottom-up only" view of human cognitive evolution, ascribed to no one in particular but described as prevalent in our field, according to which *all* human cognitive capacities must be genetically determined, with no role played by learning or culture ("only a genetic change my lead to modifications of the brain anatomy and physiology allowing for new cognitive skills required by a novel cultural practice"). In other words, neither learning nor brain plasticity play any role in the emergence of human cognitive capacities.

My first and most obvious objection to this paper is that the "bottom-up only" view that it targets is one of the tallest straw men I ever met (do you know anyone sane who supports it? Please send their names along with a quote and an email address.) This aspect of the paper clearly needs revising.

*The impression that when presenting the “bottom-up only" view we were creating a straw man was coming from a couple of sentences in which we were attributing to colleagues, without mentioning them, the idea that a causal link existed between single cultural innovations and genetic mutations. We have omitted those sentences and rewritten the introduction. In the new text we present the “bottom-up only" view as the shared assumption that a change in the genetic endowment was necessary to the emergence of the package of behavioural innovations that make us different from our phylogenetically closer relatives. Many authors share this assumption and we provide those citations throughout the introduction.

However, a lot of interesting material would remain, I think, once the straw man is out of the way. Point a) — the rise of modern human behaviors wasn't caused by the spread of H. Sapiens — is quite original and well argued. The authors adduce an exhaustive meta-analysis-like dataset concerning the emergence of dozens of distinct technologies all over the globe. This addition will be precious to researchers in many fields and is enough, I think, to justify publication. The cognitive science community will be grateful.

Concerning claim b), I am more sceptical. The author's case is, obviously, very strong for literacy, but then again no one denies that literacy is cultural through and through. (If you know anyone who does, once again, send me their email.) I am not convinced by the claim when it is made about numeracy or language — and above all I am not sure that asking "how much culture? how much genes?" is the right way to ask these questions.

*A body of empirical data supports our claim “B” about numeracy. We already quoted two reviews (Dehaene & Cohen 2007; Nieder & Dehaene 2009) that summarize those data. We have added a new one (Hannagan et al. 2015) in order to strengthen our case. The case of spoken language is indeed more controversial (see answer to next comment).

About language: the authors should either go into more detail here or refrain from raising the topic. There are many distinct components to the human language faculty (phonation; syntax; pragmatics; etc.) — I doubt one can have a meaningful debate without specifying which part of language we're talking about.

*We mention the example of spoken language only indirectly and only to make a general point about our “top-down-also” view. The reviewer is right in saying that the issue of spoken language is a complex one which would require another paper. To address this comment, we now briefly specify that cultural evolution may have affected complex syntax and semantics.

About numeracy, or "arithmetic" as it is called here: Here again it depends how we define it. "Arithmetic" usually means the mathematical manipulation of numbers, but in this paper, it is "the ability to treat exact quantitative information in a symbolic and conventional way". If it is put that way, then it is obviously right (who disagrees?). But the claim that arithmetic is cultural through and through hinges on two words in the definition, "exact" and "conventional". There's a solid case to be made from developmental & comparative psychology for a number sense for exact quantities up to 4. These numbers can be recognised and tracked fluently by babies and by many non-human species. This system's signature limits make it impossible to speak of genuine numeracy, but they also confirm the view that the system is ancient and widespread among animals. A second system can track approximate quantities beyond these small numbers, although it isn't exact.

*It seems to us that this reviewer draws a strong dichotomy between number sense, shared by may animals, and numerical symbols. Our focus is on how did we move from one to another and we argue that the step by step process eventually generating number symbols has been a cultural one and not triggered by a genetic change. We also emphasize that It is exactly the invention of such symbol systems that allows for the treatment of exact quantities much larger than 4. We have slightly changed a number of sentences to better explain this point.

The authors' view on symbolic representations of numbers are original, thought-provoking and backed by a body of justly celebrated first-hand research. Still, I am not entirely convinced by everything that is said here.
p. 14: I am not convinced that Trinil water shell or Bilzinglehben mammoth bone are indicative of symbolic ascription of meaning to symbols. Same for Les Pradelles bone. Decorative patterns do not necessarily refer to anything: see the nest decorations of Bower birds. The authors could perhaps convince me that these designs are indeed symbolic, but how could we be sure that they are numerical symbols specifically? This seems to be a stretch.

*We do not argue in our text that the Trinil shell or the Bilzingsleben bone carry numerical notations, just that they may have conveyed “iconic, indexical or symbolic” information. The same holds true for Les Pradelles.

The view that numerical graphical symbols were key to the evolution of arithmetic capacities is more debatable than it would seem at first. I defer here to the opinion of Steven Chrisomalis who wrote the book on numerical notations. As he shows, most numerical notation systems evolved as tallies, which don't, strictly speaking, involve the addition or subtraction of full numbers above 1 (a tally only computes 1 +1 +1, etc., occasionally -1). They can also represent numbers, but here again this does not make them fit for arithmetic, as traditionally defined, ie. additions, subtractions, multiplications and divisions of numbers. As Chrisomalis showed, such operations could be performed verbally long before we had practical notations to carry them out graphically. Pythagoras worked with a numerical notation system that was fit for tallying and representing numbers, but lacked proper symbols for the basic operations (let alone more complex ones). Natural language was probably enough to get arithmetic off the ground, as a first step.

*We do not claim that tallies involve arithmetic, rather the opposite. We see tallies and other forms of externalized symbol systems as prerequisite to the development of number symbols and arithmetic.

A more general problem that I encountered while reading this paper was that it seemed to hinge on a simplistic dichotomy between genes and culture. Namely, anything that cannot be accounted for by genes is assumed to be cultural. Yet there is much about human behaviour that depends on learning and plasticity in response to changing environment, without quite involving culture per se. (By culture, here, I mean traditional behaviours passed through long transmission chains that endure across generations.) It is quite possible, for all we know, that the evolution of various human capacities was favoured among other things by new environments and living conditions, without any concomitant genetic change.

*This last observation is a bit surprising because the main point of our paper is precisely to emphasize the role of learning and brain plasticity for the acquisition and transmission of cultural innovations, and promote the idea that these two factors played a prominent role in the evolution of human cognition. In other words our text is in perfect agreement with what this reviewer says here.

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Reviewer #3: Natalie Uomini

This paper is very clear, concisely written, and a broad-ranging review (including new data compiled for this ms) on archaeological and neurological data for cognitive cultural evolution. Epigenetics is here given its rightful place, as it should be. The section 3 treatment of neuroscience is excellent. The text is very well structured. I would suggest only a few minor changes as follows:

on pg. 5, line 11, the list of citations on the debate over a genetic mutation vs. gradual evolution looks like all the sources are supporting a genetic mutation of humans at 50 kya. Bruner or Wynn certainly support a gradualistic view! I suggest to rephrase the sentence to clarify that all of these citations are combined for both sides of the debate.

*We have split the citations between “gradualists” and “mutationists”, and added a few to better make the differences between the two stands.

A couple of typos in authors' names appear in the text (Draganski, Roebroeks...), please check them again.

*We have checked this

On Figure 3 and Figure 4, please label the X axes. I assume they are kyr, but it's not clear. Also, my personal preference would be to invert the direction of the X axis so that time is moving forward towards the right, as I feel it's more reader-friendly, but of course that is a stylistic matter.

*We have changed the direction of the X axis of figures 3 and 4.

The data and discussion of Figure 3 are very interesting, a valuable addition to this paper.
Please explain how you chose these categories of "cultural innovations" - perhaps a brief definition of how you define them, so that we may understand e.g. why you do not also include home-bases, long-distance transport of raw materials, or the cultural use of bird feathers. Also, please specify which hominin species are included in this dataset.

*We better explain how we choose the innovations, provide a definition of “cultural innovation” for the purpose of our paper, and specify as much as possible the hominin species included.

The list for control of fire is lacking all citations by J. Gowlett, who has arguably the most important data (Beeches Pit, Chesowanja.....), as well as latest fire results by N. Goren-Inbar (I am not sure if all of these are within your time frame of 850 kya, but it might be worth expanding the window to include these). For hafting, I would also check L. Barham's new book on this topic.

*We have added a reference to Gowlett and a new article on this topic by Sangathe. Two papers by N. Goren-Ingar are already in the list of references. We have also added L. Barham book in the references

On page 14 you mention Bilzingsleben, but I would cite that with caution, given all the works by C. Pasda and colleagues showing that the site was mostly natural and that nearly all of the supposed cultural artifacts were not human-made.

*We have added this reference. However, this study does not demonstrate that the site is natural, just that there is a previously undetected natural component in it.

Overall the ms is a joy to read!

Figure 1

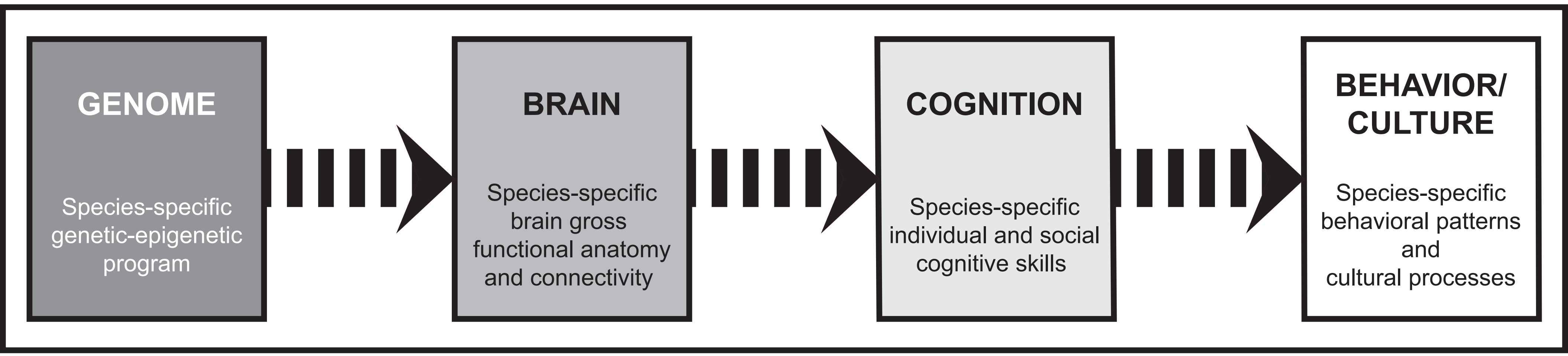

GENOME
Species-specific genetic-epigenetic program
BRAIN
Species-specific brain gross functional anatomy and connectivity
COGNITION
Species-specific individual and social cognitive skills
BEHAVIOR/ CULTURE
Species-specific behavioral patterns and cultural processes

Figure 2

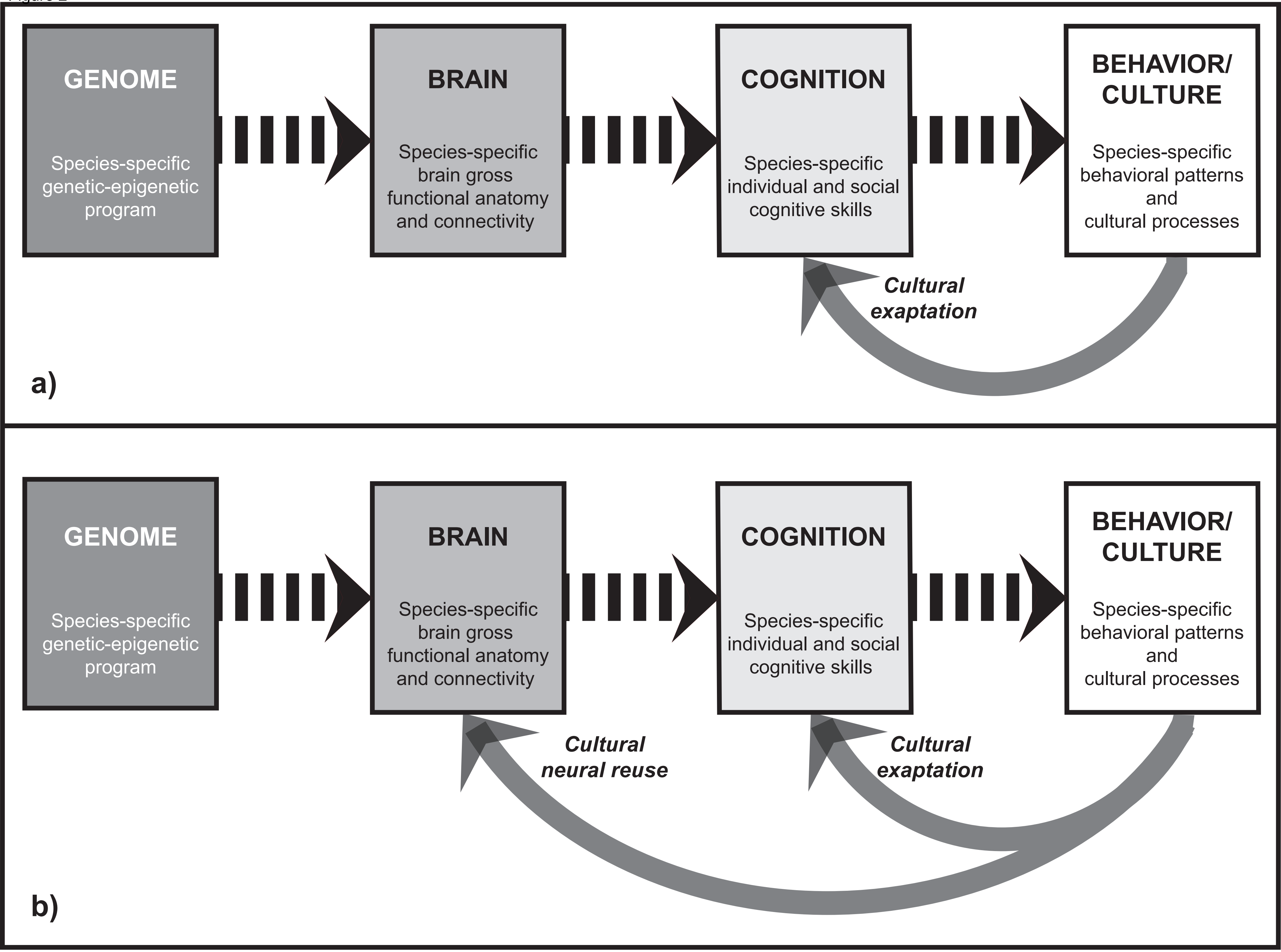

GENOME
Species-specific genetic-epigenetic program
BRAIN
Species-specific brain gross functional anatomy and connectivity
COGNITION
Species-specific individual and social cognitive skills
BEHAVIOR/ CULTURE
Species-specific behavioral patterns and cultural processes
Cultural exaptation
a)
GENOME
Species-specific genetic-epigenetic program
BRAIN
Species-specific brain gross functional anatomy and connectivity
COGNITION
Species-specific individual and social cognitive skills
BEHAVIOR/ CULTURE
Species-specific behavioral patterns and cultural processes
Cultural neural reuse
Cultural exaptation
b)

Figure 3

Click here to download Figure Colage_Derrico_Topics_Figure3.tif

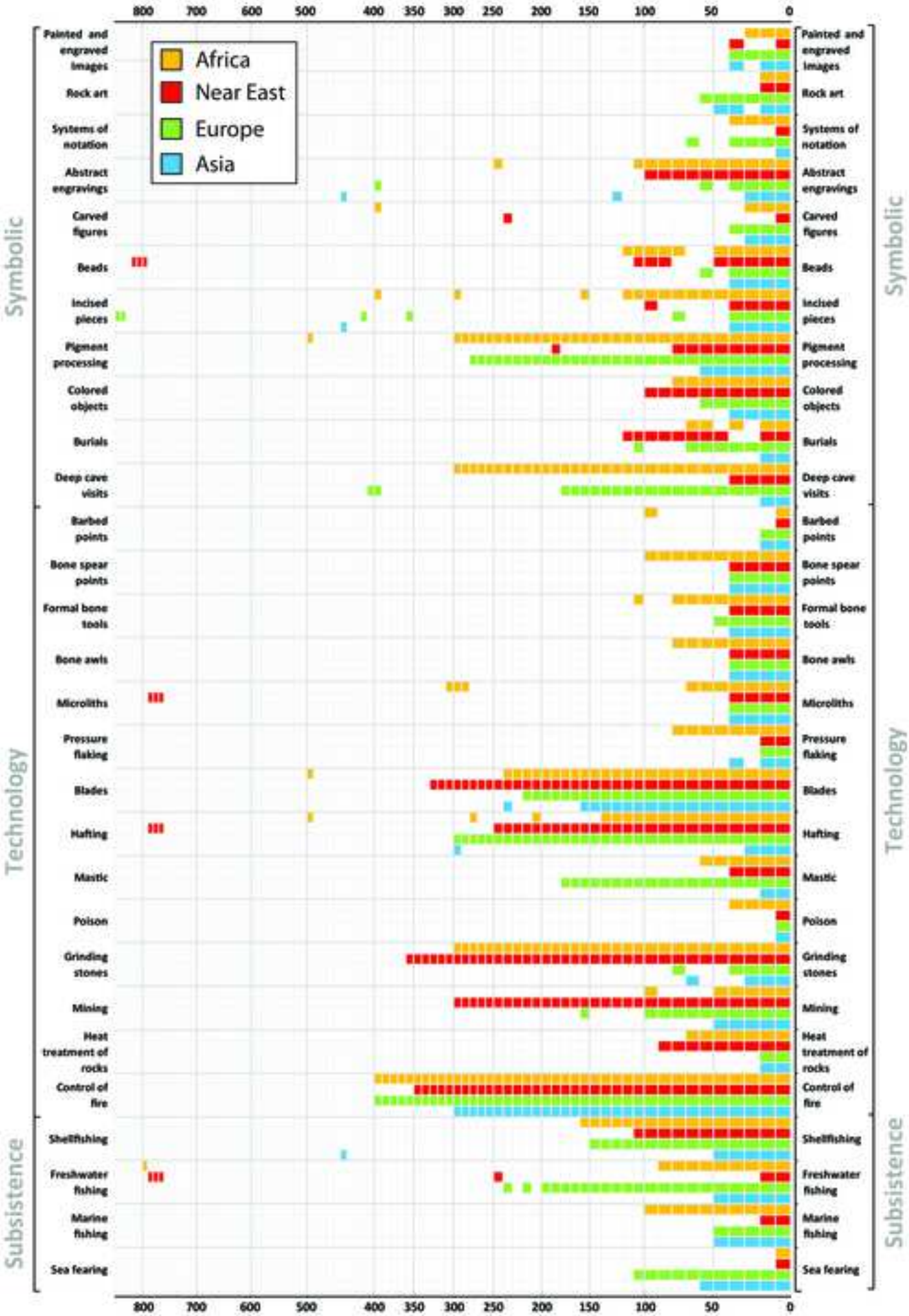
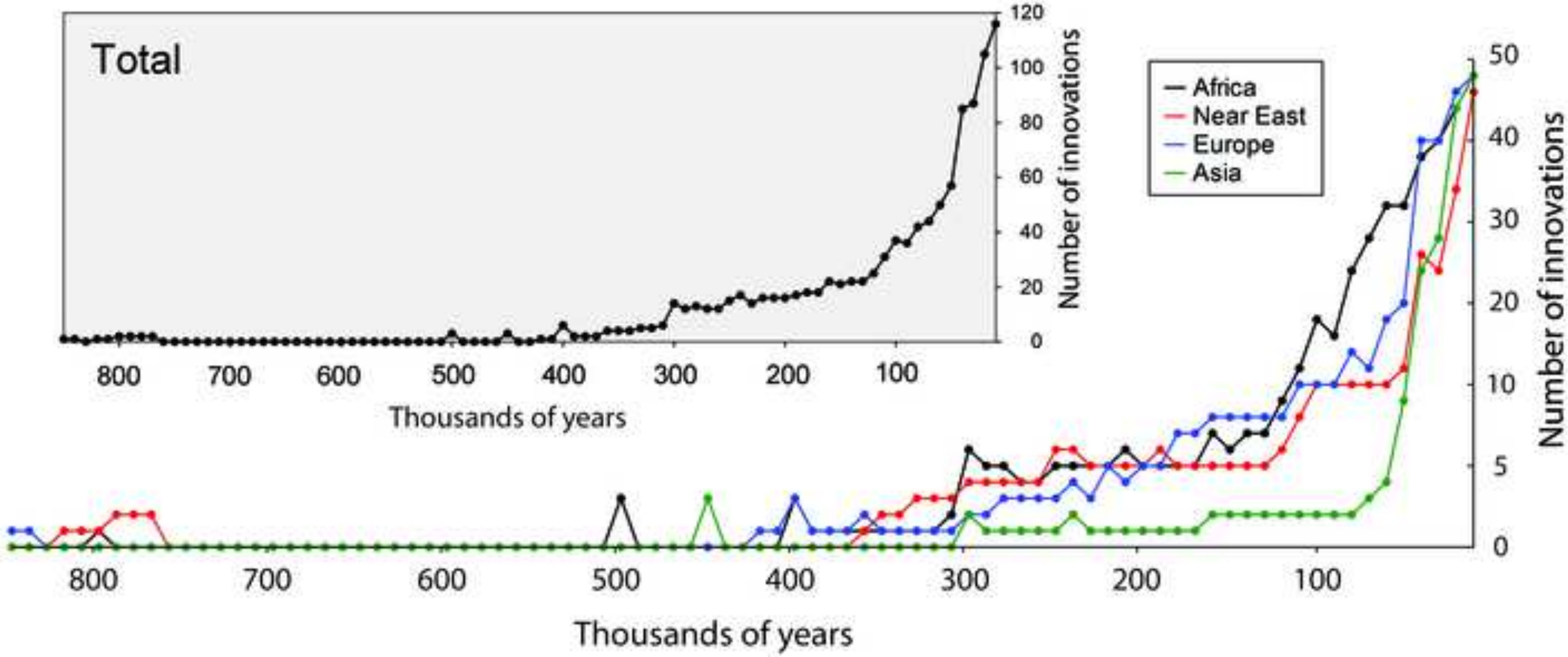


Figure 4

Click here to download Figure Colage_Derrico_Topics_Figure4.tif



Supplementary Material

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Topics in Cognitive Sciences

Culture: the driving force of human cognition

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Painted/engraved images

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