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On human evolution by means of self-domestication:
A review

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Resumen

La domesticación ha sido históricamente considerada como un proceso plenamente dirigido por los humanos. Sin embargo, la visión que se está haciendo cada vez más prevalente en la literatura científica es la de varías vías de domesticación. Mientras que algunas de estas vías habrían sido simplemente fruto del comensalismo, siendo el resultado de presiones selectivas, otras habrían requerido de un proceso dirigido. Indistintamente de la vía de domesticación seguida, los animales domesticados resultantes parecen compartir una serie de características fenotípicas que constituyen el llamado síndrome de la domesticación. El experimento de Belyaev probó que el síndrome de la domesticación se podía inducir a partir de la selección contra la agresividad, por lo que la selección contra la agresividad habría sido el mecanismo evolutivo para la aparición de todos los domesticados. La observación de rasgos del síndrome en humanos ha llevado a algunos autores a plantear la posibilidad de que, dadas las condiciones, la docilidad podría haber sido una característica favorecida por la selección natural en nuestra especie. Este suceso, bautizado como autodomesticación humana, habría tenido lugar a lo largo del Paleolítico, produciendo importantes cambios morfológicos, cognitivos y culturales en nuestra especie.

Abstract

Domestication has long been understood as a process resulting from full human intentionality. However, the vision that is becoming more extended in the scientific literature is the one regarding more than a single pathway to domestication. While some of these pathways would have been the result of commensalism, being the outcome of selective pressures, others would have required a human directed process. Regardless of the followed pathway, all domesticated animals seem to share certain phenotypic traits, which constitute the domestication syndrome. Belyaev's experiment probed that domestication syndrome could be induced by selection against aggression, implying that this would have been the evolutive mechanism for the origin of all domesticates. The observation of domestication syndrome traits in humans has led some authors to propose that, given the appropriate context, tameness could have been positively selected by natural selection in our species. This event, called human self-domestication, would have taken place during the Palaeolithic, producing critical morphological, cognitive and cultural changes in our species.

1. Introduction

Culture understood as the capability of learning and transmitting sets of abilities which range from hunting to social communication, and which develop differently in distinct populations within the same species, is non-exclusive to the human species (*Homo sapiens*). It has been observed in a wide variety of animals, from our closely related chimpanzees (*Pan troglodytes*) (Whitens, 2011) to evolutionarily more distant animals such as cetaceans (Filatova et al., 2017). However, it is in the human species where it has attained its highest complexity, being established a tight bond between cultural and brain evolution (Gintis, 2011; Street et al., 2017; Van Schaik & Pradhan, 2003). One of the products of this evolution was the process of domestication, which marked the start of modern human societies in the Neolithic (Bocquet-Appel, 2011). Ironically, some kind of domestication process which authors refer to as "self-domestication" may have been critical during our own evolution, implying morphological and behavioural changes which may have influenced the brain-culture coevolution (Cieri et al., 2014). In this work I will assess the correlation between domestication and self-domestication, and review how the later fits into the human evolutionary history.

1.1 Domestication

According to mtDNA data from current human populations, the first known members of our species must have lived in Africa over 200,000 years ago (Cann et al., 1987). The picture presented by fossil evidence is however more complex. The previously oldest known fossils pointed to the origin of our species being sometime 160,000-154,000 years ago (White et al., 2003), but more recent studies have pushed the date back to the 300,000 years ago (Hublin et al., 2017), not only spreading the debate about the date of origin, but also about the place. Either the way, the earliest signs of animal domestication did not appear until much more recently in human evolutionary history, over 10,000 years ago (Diamond, 2002; Larson & Dorian, 2014; Zeder, 2012).

Dogs seem to have been the first species to become domesticated. It is now clear that they evolved from wolves (*Canis lupus*), but it is still a topic of hot debate when and where did they become domesticated (Thalmann & Perri, 2018). Although some authors propose dates ranging from the 20,000 to the 40,000 years ago, these dates are still debatable, so it is still the safest to just assume that dog domestication occurred in hunter-gatherer societies, prior to the domestication of other animals and sometime between 15,000-12,000 years ago (Thalmann & Perri, 2018). Of more relevance to this work is however how did it occur instead of when and where. Zeder (2012) identified that evolutionary explanations for domestication fell either into a completely human directed process (with a clear discontinuity in the human-animal relationship between pre-pastoral and pastoral communities) (e.g., Meadow, 1989) or by contrast into just a mutualistic relationship between species characterised by gradual change and without any intentionality to the process (e.g. Rindos, 1989). Acknowledging that in fact domestication is one type of mutualistic relationship, but remarking the importance of human intentionality to certain aspects of the process, Zeder (2012) proposed three different pathways to domestication, ranged from the less to the most directed: the *Commensal Pathway*, the *Prey Pathway* and the *Directed Pathway*.

a) The *Commensal Pathway* describes how certain animals may have benefitted from scavenging the wastes produced by human populations, or feeding on the animals attracted to them (Zeder, 2012). Animals which would have been domesticated this way include the dog, the cat and possibly the pig (Zeder, 2012). This pathway is easy to infer by observing how nowadays human populations attract wildlife for its resources in the form of human wastes (Harveson et al., 2007; Peterson et al., 2004) however, back in the times of hunter-gatherer societies this pathway would have required longer periods of human residential permanence, which seem to have occurred during postglacial periods in the Late Pleistocene (Zeder, 2012). It is most likely that wolves, animals which directly competed with humans for resources and even were aggressive towards them followed this pathway, instead of a direct one as proposed by authors such as Galton (1907) (Larson & Dorian, 2014). Upon observation of modern hunter-gatherer populations keeping wild animals as pets, Galton (1907) proposed that wolf domestication may have occurred by ancient hunter-gatherers keeping found wolf puppies as pets. However, it is been observed that pet keeping in modern hunter-gatherer populations has not led to any kind of domestication (Serpell, 1989). The *Commensal Pathway* provides a plausible explanation for wolf domestication, as the less aggressive and human-tolerant members of the pack would have seen their fitness improved within the human niche (Driscoll et al., 2009; Hare et al., 2012; Zeder, 2012). As closer bonds with their human hosts started developing, humans took a more active role in the dog domestication process, but for that time the domestication syndrome traits had already appeared (Morey, 1992; Trut, 1999; Zeder, 2012). This pathway is the one of most interest to us in this work, as it shows the evolutionary process leading to the domestication syndrome can take place without direct human intervention, just by selective pressures.

b) The *Prey Pathway* suggests that when human pressure upon the animals that were hunted for meat became excessive, game-management strategies would have arisen in order to keep a sustainable population of preys. Without any intentionality to domesticate the animals, these game-management strategies would have slowly turned over time into herd-management strategies, with humans controlling the movement, feeding and reproduction of the prey population, becoming in the end a completely human directed process. Such pathway would have been followed for instance by most major livestock species (Zeder, 2012).

c) The *Directed Pathway* establishes direct human intervention and intentionality in the process of domestication. It probably came into being after the other two pathways, when human populations had already realised wild animals could be tamed. The horse would be an example of animal following this pathway (Zeder, 2012).

1.2 Belyaev's foxes

Regardless of the pathway followed to domestication, all domesticated species have certain traits in common which seems that were fixed during early stages of the process, such traits include changes in coat pigmentation and behaviour, shifts in developmental timing, alterations in the shape of the skull and body size, brain size reduction and paedomorphism. (Belyaev, 1979; Clutton-Brock, 1999; Hare et al., 2012; Larson & Dorian, 2014; Sánchez-Villagra et al., 2016; Trut, 1999; Wilkins et al., 2014). All these changes constitute a phenotypic convergence which authors refer to as the "domestication syndrome". Historically, this phenotypic convergence was already acknowledged by Darwin (1868), however, due to the difficulty of embodying the cases of all domesticated animals into a single empirically testable theory, the models trying to explain its emergence treated the case of each animal separately and considering full human intentionality to the process, such as in the aforementioned model proposed by Galton (1907) for dog domestication (Larson & Dorian, 2014).

It was not until the 1950's that a single experiment changed the views on animal domestication. The Russian biologist Dmitry Belyaev hypothesized that animal domestication had been the result of human unintentional selection for a single trait: tameness. Considering the vital role of the neurohormonal system in the ontogeny of higher vertebrates, he hypothesized that selection upon a trait that was controlled by it could produce the shifts in the ontogeny that led to the domesticate traits as byproducts. In order to test his hypothesis, Belyaev designed an experiment in which from a population of wild silver foxes (*Vulpes*

vulpes) he would breed only the ones that were not aggressive and fearful towards human, the control group being bred randomly. By the sixth generation, the emergence of dog-like prosocial behaviours in the selected foxes led to the establishment of a new category, in which selection took place not only on those that were not aggressive and fearful, but which also showed a positive response to human contact. The experiment started in 1959 (in 2019 it is still running), and by 1999, with over 30-35 generations of directed breeding, the resulting foxes were very different from the initial ones. Not only did they differ in coat pigmentation, but their snouts had become shorter, their tails and ears floppy and their playful behaviour resembled more the one of dogs rather than wild foxes (Fig. 1) (Belyaev, 1979; Trut, 1980, 1999; Trut et al., 2009). Belyaev's experiment resulted in a plausible explanation for animal domestication. Selection for tameness, unintentional in some cases and intentional in others, would have resulted in the domestication syndrome that characterises all domestic animals.

Figure 1. On the left a silver fox resulting from selection for tameness during Belyaev's experiment, with derived phenotypic traits and showing prosocial behaviour. On the right a juvenile silver fox with wild phenotypic traits, showing a negative response to human contact. Belyaev's foxes show many of the anatomical traits that are attributed to the domestication syndrome, but most notably, their behaviour has shifted from the one of wild animals to a pro-social one, like the observed in dogs. **Sources**: Left image was taken from American Scientist and its authorship corresponds to Lyudmila Trut and the Institute of Cytology and Genetics of Novosibirsk. Right image was taken from www.msn.com and its authorship corresponds to Darya Shepeleva.

1.3 The domestication syndrome

The way in which current research is addressing the domestication syndrome can be expressed as the study of changes into four major categories (Hare et al., 2012). These categories comprise physiological, behavioural, anatomical and cognitive changes (the limits among them being many times diffuse).

a) The physiological changes include shifts in mechanisms related to aggression and stress responses (Hare et al.,2012). An example of these changes can be observed in Künzl et al. (2003) experiment comparing the response of domestic guinea pigs (*Cavia aperea* f. *porcellus*) and their wild counterparts (*Cavia aperea*). Their results showed that domestic guinea pigs exhibited lower cortisol levels than their wild counterparts when exposed to a stressful situation, which is indicative of changes in the HPA (hypothalamic-pituitary-adrenal) system (Künzl et al., 2003). Other observed physiological changes are involved in the alteration of the reproductive cycle. In wild forms reproduction takes place seasonally, whereas in domestic ones it can take place at any moment of the year (Trut; 1999).

b) The behavioural changes observed in domesticated animals are mainly the result of the aforementioned physiological changes. They mainly comprise reduced aggression and increased pro-social behaviours (Hare et al.,2012). For instance, Künzl et al. (2003) observed lower frequency of aggressive behaviours in the domestic guinea pigs than in their wild counterparts. Reduced aggression and increased pro-sociality are also among the most notable results of Belyaev's experiment (Belyaev, 1979; Trut, 1980, 1999; Trut et al., 2009).

c) Anatomical changes include snout shortening, reduction in the sexual dimorphism of the crania, floppy ears and coat depigmentation (Fig. 2) (Hare et al., 2012; Wilkins et al., 2014). They constitute the most notorious phenotypic changes of the domestication syndrome, and they all have in common their origin from neural crest cells (Wilkins et al., 2014).

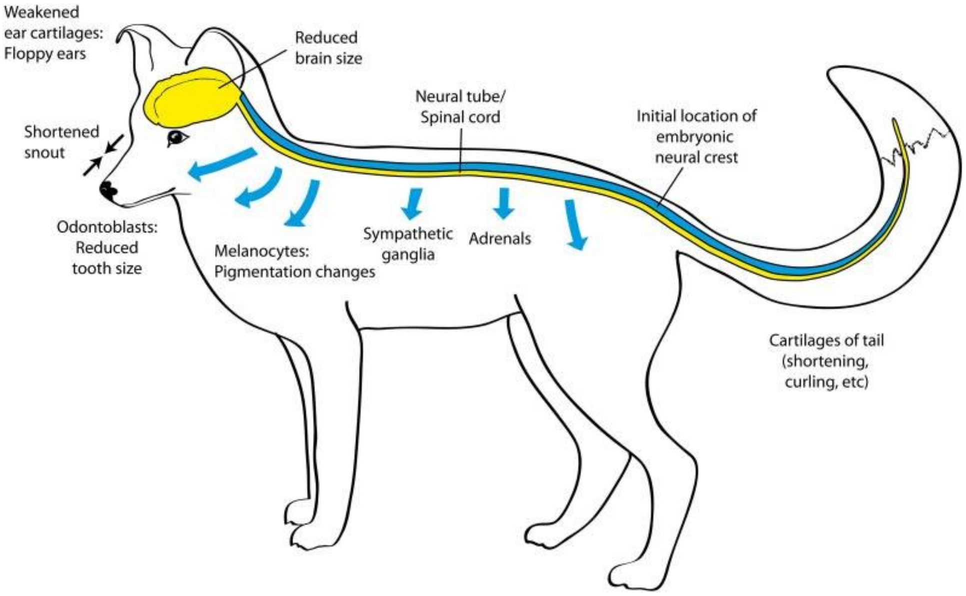

Figure 2. The set of changes anatomically observed in the domestication syndrome seem to be tightly linked with neural crest cells development and differentiation, and are probably the result of shifts in gene expression during ontogeny. **Source**: Image taken from Wilkins et al. (2014).

d) The cognitive changes refer to the increased social problem-solving skills and sociocognitive abilities observed in domesticates when compared to non-domesticates (Hare et al., 2012). Dogs are a classic example for their high performance in these types of tasks. When interacting with humans they do outperform wolves, but also chimpanzees, which could be argued that given their evolutionary proximity to humans would perform better (Hare et al., 2002). There has been debate in whether these abilities are a byproduct of selection for tameness (and therefore part of the domestication syndrome) or the result of direct selection for these particular skills (Hare et al., 2005). Running the same kind of experiments with Belyaev's foxes has showed them to perform similarly to dogs, outperforming wolves and untamed foxes, which supports the idea of social problem-solving skills to be a byproduct of selection for tameness (Hare et al., 2005). This view is further supported by experiments with goats, animals in which directed selection has focused on production, but which also rely on human communicative gestures (Nawroth et al., 2016)

1.4 Self-domestication

If the conditions in which a tame behaviour could be positively selected occurred in nature, would the domestication syndrome develop in wild species just by natural selection?

This is the question that some authors have raised upon observation of domestication syndrome traits first in bonobos (*Pan paniscus*) (Hare et al., 2012) and then in humans (Cieri et al., 2014; Franciscus et al., 2013). In Belyaev's experiment, the domestication syndrome was the result of a human directed process. As mentioned before, animals such as dogs seem to have undergone the same process just by the action of selective pressures (although this pressure was interspecific, due to unintentional human influence). But now a third option opens up, with just intraspecific pressures being responsible for the domestication syndrome. As no formal definition for the term "self-domestication" has yet been established, it is being used for describing many domestication processes without human intervention, including dog domestication. As for such cases I have already addressed them as domestication through the *Commensal Pathway*, I will be using the term self-domestication exclusively for the bonobo and human hypotheses.

Bonobos are closely related to chimpanzees, constituting both of them the two single species of the genus *Pan*. However, they differ significantly in their behaviour and psychology (Hare et al., 2012). Chimpanzees are characterised by high levels of aggression, which they use towards members of the same group or towards members of other groups in order to show dominance, fight for resources and defend their territory (Goodall, 1986; Muller, 2002; Muller et al., 2007). Male aggression towards females is also common, and encounters between groups can result in infanticide (Muller, 2002; Muller et al., 2007).

On the other hand, aggression does not play such an important role in bonobos. Males do not show severe aggression towards other males within the group, and displays of aggressive behaviour are rare (Kano, 1992; Parish, 1996). Infanticide appears to be absent or extremely rare (Gruber & Clay, 2016) and the same goes for intragroup killing (Furuichi, 2011). Encounters between members of different groups often result in prosocial behaviours, such as food sharing (Tan et al., 2017). Aggression from males to females is also rare, and if given the case a coalition of females tends to defend the attacked one (Kano, 1992; Parish, 1996). This also happens to be one of the cases in which bonobos can get to be aggressive (Parish, 1996). Regarding cognitive aspects, in tests based on reading behavioural intentions such as the ones mentioned in the domestication syndrome chapter, bonobos outperform chimpanzees and perform more similarly to dogs, as also seen with Belyaev's foxes (Herrmann et al., 2010). All these behavioural traits along with morphological characteristics such as reduced cranial size, reduced prognathism, diminished cranial sexual dimorphism, developmental delays (paedomorphic cranium), canine size reduction in males and females, white tail tuffs (in juveniles) and pink lips fall within the sets of traits characteristic to the domestication syndrome (Coolidge, 1933; de Waal & Lanting, 1997; Hare et al., 2012; Kelley, 1995; Liebermann et al., 2007; McHenry, 1984).

Considering all of the above, the hypothesis that bonobos evolved through selection for tameness is a plausible one, however it is no clear how it might have occurred. Based on their current ecology, what Hare et al. (2012) propose is that after isolation by the Congo River bonobo ancestors were set in an area of high density of resources due to the absence of gorillas (*Gorilla gorilla*) as competitors. It is in such context were female bonobo groups would have been able to remain together (female chimpanzees tend to go alone when resources are scarce), being more capable of repelling male aggressions and sexual coercion, and having the chance of being selective.

The current human self-domestication hypothesis follows a similar approach, identifying domestication syndrome traits in humans and discussing the possible selective pressures which could have originated them. The rest of this work will be based on reviewing and discussing this hypothesis.

2. Objective

The objective of this work is to review in a critical way the human self-domestication hypothesis, being the main objectives:

- To determine whether the data and model presented by Cieri et al. (2014) are consistent and of interest for the study of human evolution.
- To identify the current state of the human self-domestication hypothesis and its future perspectives.

3. Methodology

The current work is the result of a bibliographical research on the human self-domestication hypothesis. The flux diagram, representing how the initial bibliographical search leading to Cieri et al. (2014) as main article was done, can be seen in Figure 3.

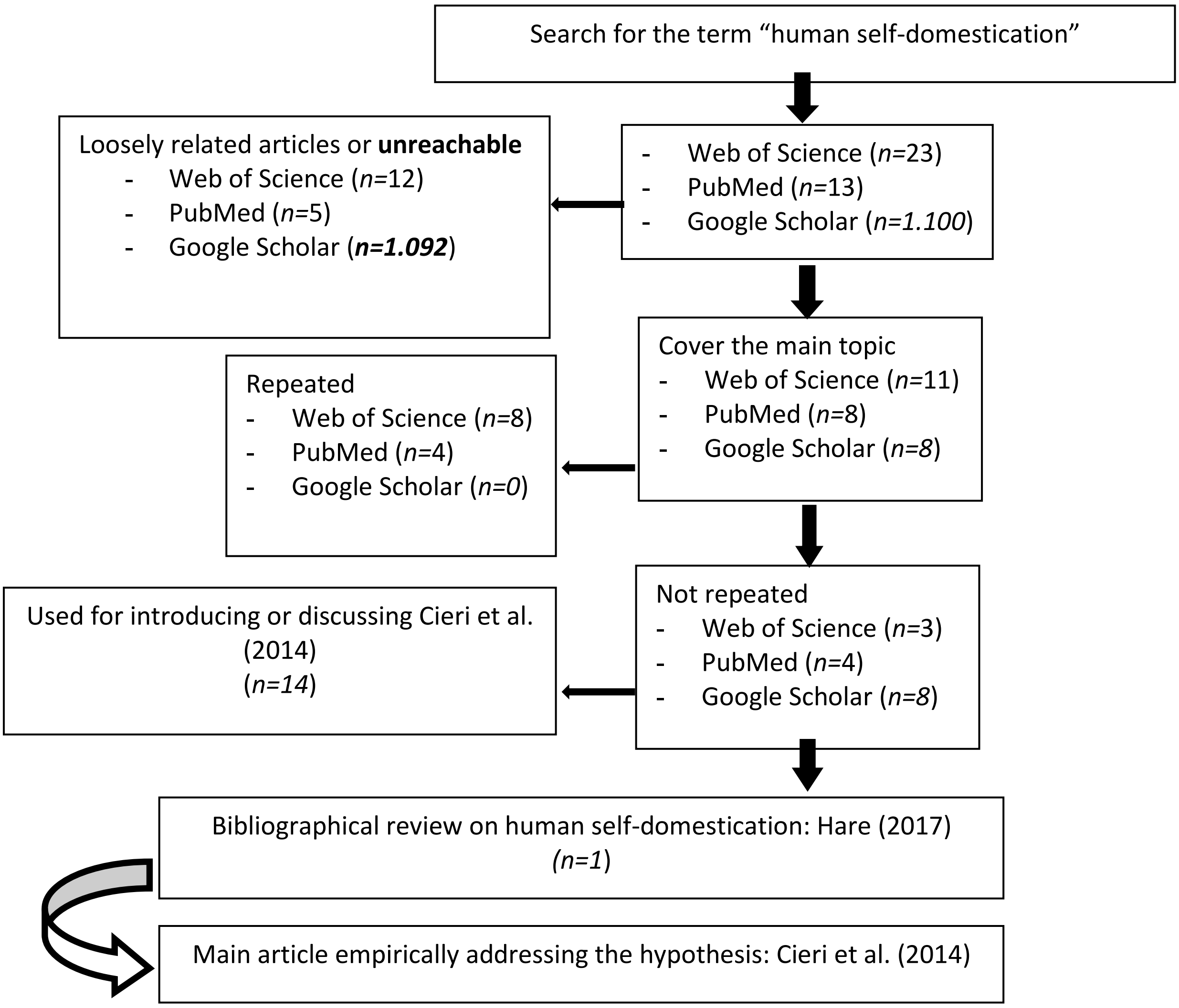

Figure 3. Flux diagram of the main bibliographical search. Cieri et al. (2014) was found in the bibliography of Hare (2017).

Cieri et al. (2014) was defined as the main article for it being the first one to address the human self-domestication hypothesis (the one within Belyaev's line of thought) in an empirical way. After reading the main article and others resulting from the initial search, further bibliographical searches were focused to finding introductory articles, which set the context and line of thought for the main article; and discussion articles, which argued against the hypothesis or supported its vision with additional data.

Introductory articles included studies on animal domestication, most of which were provided by the research directors (Prof. Rebato & Dr. Jelenkovic) as guidance materials at the beginning of the research; studies on the domestication syndrome and articles regarding Belyaev's experiment. Searches for these articles included terms such as "domestication syndrome", "self-domestication" and "Belyaev foxes". Articles resulting from the searches were selected after considering that their titles and abstracts fitted in the context given by the articles of the initial search.

Discussion articles included some of the results of the initial search, but also recent articles that had been published through the year, which were found by repeating searches for the terms "self-domestication", "human self-domestication" and "domestication syndrome". Discussion articles were also the result of specific searches in order to contrast Cieri's et al. (2014) data. Such searches included "supraorbital torus diet", which led to searching for the term "masticatory functional hypothesis". The other specific search was for the term "brain size testosterone". These searches led to the articles for discussing brow ridge function and the role of testosterone in brain volume respectively.

For both introductory and discussion articles, the bibliographical references found within the literature proved to be important sources of authors and studies which may have not been found otherwise.

4. Results

Although not the first ones to talk about human self-domestication, nor to address human cranial gracilization, Cieri et al. (2014) were the first ones to address the current concept of human self-domestication (within Belyaev's line of thought) also proposing a whole evolutionary context for it.

Cieri et al. (2014) based their study on the idea that the craniofacial feminization occurring between archaic *Homo sapiens* and anatomically modern humans (AMH) is the result of a reduction in androgen reactivity starting in the Middle Stone Age/Middle Paleolithic. This reduced androgen reactivity would be the result of behavioural adaptation to higher social tolerance, positively selected for its implications in high population densities, complex social networks and cultural interchange. Craniofacial feminization would therefore be linked to the emergence of behavioural modernity, which is marked by the emergence of a wide array of new technologies and the first evidences of abstract thinking about 50 Ka BP.

In the study they analyzed three sets of human male crania (where changes in androgen levels would be more evident) pertaining to three different time periods: the Middle Stone Age/Middle Paleolithic (13 samples, from 200 to 90 Ka BP), the Later Stone Age/Upper Paleolithic (41 samples, from 30 to 10 Ka BP) and the Holocene (1367 samples, 10> Ka BP); the Holocene samples being further divided into “Foragers” and “Agriculturalists”. Due to the lack of samples, 6 of the 13 used MSA/MP samples were possible female crania (not clearly identified).

The variables they measured were facial shape, brow ridge projection and endocranial volume (ECV). Facial shape and brow ridge projection were measured as indicators of the androgen levels. ECV was measured for two reasons: to control the effect of head size for the other two measures, and to assess if the domestication syndrome trait of reduced cranial size also applied to humans.

To measure facial shape, they used an index based on scaling bizygomatic breadth (ZYB) and nasion-prosthion height (NPH) (Fig. 4). To measure brow ridge projection, they used an index based on summing supraorbital projection (SOS) and glabellar projection (GLS), then scaling the result by the bifrontal breadth (XFB) (Fig. 4). For the ECV they extracted already published data from the samples they were using, and in the cases in which they lacked it, they estimated it from cranial dimensions using a male specific formula (Lee and Pearson, 1901).

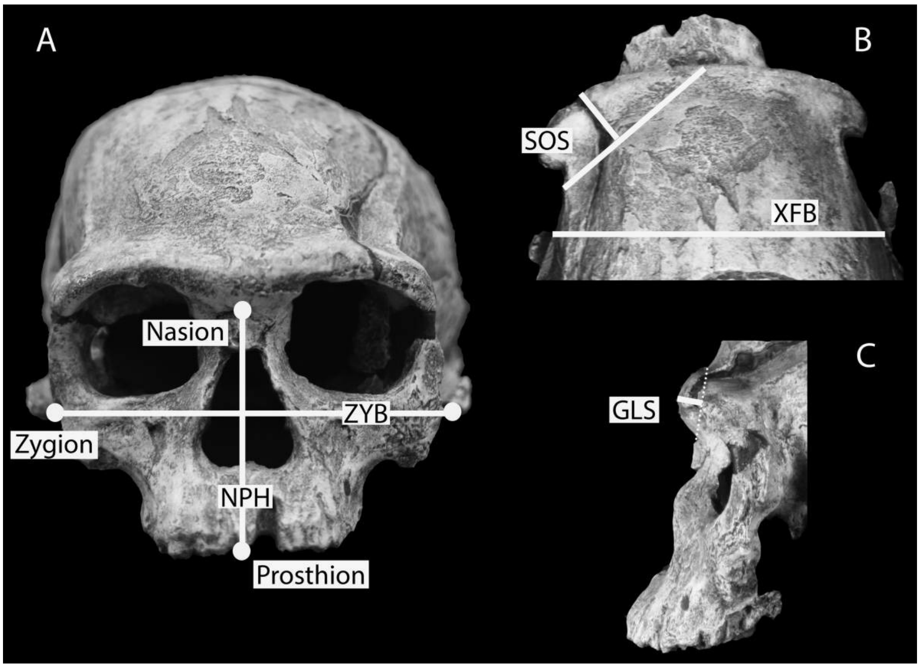

Figure 4. Display upon a cast of the measurements taken by Cieri et al. (2014) for facial shape and brow ridge projection determination. ZYB: bizygomatic breadth; NPH: Nasion-prosthion height; SOS: supraorbital projection; XFB: bifrontal breadth; GLS: glabellar projection. **Source**: Image taken from Cieri et al. (2014).

Cieri's et al. (2014) results for brow ridge projection and facial shape are summarized in Figure 5, being expressed in terms of percent of feminization. The general trend observed in Figure 5 is a decrease in facial masculinity from the MSA/MP onwards. The biggest difference is seen between the MSA/MP and the LSA/UP, with an increasing degree of feminization for both the facial shape and the brow ridge projection. From LSA/UP to recent human foragers the degree of feminization in the facial shape remains the same, but it is increased regarding the brow ridge projection. Between recent human foragers and recent human agriculturalists, brow ridge projection is slightly more feminized (not significantly though), but facial shape is more masculinized. The height of the rectangles that are next to the crania represent the proportional difference in absolute brow ridge projection relative to the samples of recent humans. There is a trend of decreasing height in the rectangles from MSA/MP to LSA/UP and to recent humans. The diamonds on the other hand represent the proportional difference in facial height (NPH; diamond's height) and the proportional difference in in facial width (ZYB; diamond's width). Both height and width are reduced from MSA/MP to LSA/UP. However, between MSA/MP and recent humans the difference is not distinguishable.

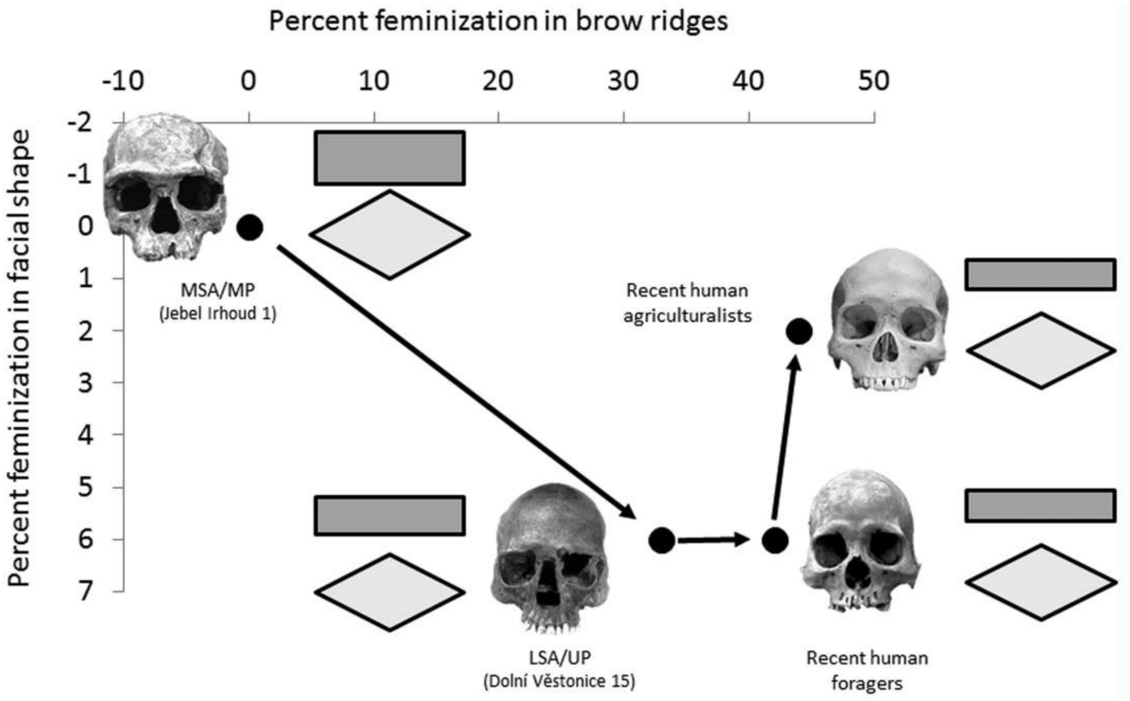

Figure 5. Mean degree of feminization (in %) for brow ridge projection and facial shape in the four sets of crania. The shapes next to the crania represent the proportional difference in brow ridge projection relative to recent humans (rectangle height) and the proportional differences in facial height and width (diamond's height and width respectively). **Source**: Image taken from Cieri et al. (2014).

The mean results for ECV are gathered in Table 1, and they show no clear trend from the MSA/MP to recent humans. LSA/UP sample shows an increase in ECV from the MSA/MP, but then a decrease to previous levels in modern humans.

Table 1. Mean endocranial volume in each of the samples. Data extracted from Cieri et al. (2014).

Sample	MSA/MP	LSA/UP	Foragers	Agriculturalists
Mean ECV (cm^3)	**1457**	**1533,6**	**1451,57**	**1464,6**
SD	118,1	103,9	103,2	85,9
n	12	31	422	945

Cieri et al. (2014) considered their results to be consistent with their hypothesis. Brow ridge projection reduction and feminization of the facial shape would indicate a reduction in androgen levels, and consequently a reduction of aggression and an increase of prosocial behaviours, which would be an adaptation to higher population densities. As for the case of the facial shape index being more masculinized in agriculturalists than in foragers, they explained that the general trend over time seems to have been a reduction in the facial length;

however, a moderate increase in agriculturalists' facial length and narrowing of the facial width (which they attributed to a reduction in prenatal testosterone levels) is what is pushing the facial shape index towards archaic humans in agriculturalists. Authors also claimed not to be aware of any physiological basis for linking ECV with androgen reactivity, thus explaining the ECV results.

5. Discussion

5.1 On Cieri et al. (2014)

Cieri's et al. (2014) work is remarkable in the way it creates an integrative context for the human self-domestication hypothesis. The authors did not limit themselves to explain a phenotypic change from the view of physical anthropology, but went further beyond and treated this phenotypic change just as one of the evidences of the emergence of human behavioural modernity, thus encompassing many separate fields such as physical anthropology, physiology, genetics, behavioural sciences, linguistics and archaeology. Their model drinks from the bonobo self-domestication hypothesis (Hare et al. 2012) (and therefore from Belyaev's experiment), and provides a context in which the decreased levels of aggression due to high population densities and more complex social networks would have encouraged increased prosociality (cooperation), and with it cultural and technological sharing (with the consequent fitness increase and the development of behavioural modernity).

The model is nevertheless not exempt for criticism, its main flaw being already pointed by commentators to the article. Through their whole work, Cieri et al. (2014) invoked high population densities as the factor motivating selection for less aggressive individuals (selection acting upon males mainly) and therefore with increased social tolerance. Wrangham (2014) pointed the lack of an explanation for how high population densities would have promoted social tolerance, and signaled the study of Thierry (2007) combined with data of Jones et al. (2009) to show that no such causation is given in *Maccaca*, and neither in bonobos (Balcomb et al., 2000; Fruth et al., 2008) were population densities seem to have no correlation at all with social tolerance. Commentators Steele & Weaver (2014) also pointed the example of Blombos Cave as troubling to Cieri's et al. (2014) model. Blombos Cave in South Africa has some of the best evidences of behavioural modernity of the whole MSA, however, published data supports low population densities rather than large ones (Klein & Steele, 2013). Altogether, these evidences made Cieri's et al. (2014) model based on high population densities not very promising. The authors acknowledged this fact in their final reply to commentators, and suggested that other mechanisms may have actually promoted social tolerance, such as the need of increased male-male tolerance for establishing complex social networks among hunter-gatherer groups, rather than high population densities.

Within the field of physical anthropology, Cieri's et al. (2014) work provided a new explanation for the reduction of cranial robusticity through the Paleolithic, which to the moment had been mainly explained from the perspective of the masticatory-functional hypothesis (Carlson, 1976). This hypothesis proposes that the recent change in cranial robusticity is the result of shifting from the hunter-gatherer to the agriculturalist diet. This shift towards a soft diet would have reduced stress upon facial muscles and therefore suppressed the need of strong and robust facial bones. Regarding the supraorbital torus, or brow ridges, some authors such as Russell (1985) acknowledged the various functions it can have, but remarked resistance to bending stress during mastication as the principal one. According to Russel (1985), development of the supraorbital torus would be tightly linked to supporting masticatory pressures, being the role of endocrine factors secondary. Although it is evident that many cranial morphological features have been shaped due to dietary adaptations not only during primate evolution, but during the whole vertebrate evolution (Dumont et al., 2016; Kelley & Motani, 2015; Makedonska et al., 2012), Cieri's et al. (2014) model may proof an exception to this general trend. Cieri et al. (2014) pointed to Lieberman (2011) as evidence for the stress being supported by the supraorbital torus during mastication to be insignificant when compared to the stress being supported by the zygomatic arches or the mandible. Therefore, a moderate supraorbital torus would be enough to resist the stress produced by mastication, and its development would not be as tightly linked to dietary adaptations as previously thought. Further support for Cieri's et al. (2014) model can be found in their own data. If hunter-gatherer diet required of more robusticity in the supraorbital torus than the agriculturalist diet, we would expect the results showed by Cieri et al. (2014) to show so. However, the differences they found in the supraorbital torus between current agriculturalist and hunter-gatherer populations were not significant, which argues against the idea of the supraorbital torus being reduced in the transition from hunter-gatherer to agriculturalist populations. Nevertheless, this would not imply whether other bone structures of the crania had been modified or not during the dietary transition.

Regarding the ECV results, Cieri et al. (2014) argued not to be aware of any physiological basis for relating ECV with androgen reactivity. Although there may not be articles directly linking androgen reactivity with ECV as such, there are indeed multiple studies that relate testosterone with volume increases/reductions in distinct areas of the brain and at different stages of the life cycle (Heany et al., 2016; Herting et al., 2014).

Hare (2017) further addressed the question of brain size within the human self-domestication hypothesis by proposing that other major evolutionary forces may have acted increasing it, and therefore acting against the brain size reduction the domestication syndrome would have promoted. However, the fact that Cieri's et al. (2014) results on ECV did not reflect in recent human evolution the process of brain size reduction observed in other domesticates as part of the domestication syndrome does not suppose a priori a problem for the hypothesis of human self-domestication. Sánchez-Villagra et al. (2016) already addressed how the domestication syndrome traits are not universal to all domesticates, and its modularity and flexibility not even close to be understood. This view has been further supported by recent research on the domestication syndrome carried out by Wheat et al. (2019). Their research in ancient and modern dog breeds has noted that certain characteristics of the domestication syndrome can be selected for or removed without altering the other characteristics. According to the authors, their results show the domestication syndrome works by multiple independent factors rather than a single physiological pathway. A personal interpretation is that selection for tameness (such as in Belyaev's experiment) acts upon regulatory genes early expressed during ontogenesis and which therefore have a cascade effect. The arrange of genes affected by this cascade effect may have varied throughout species due to differences in gene expression and regulatory pathways. Given the results of Wheat et al. (2019), it also seems clear that the existence of more than a single physiological pathway has allowed selection to act upon discrete traits of the domestication syndrome. Therefore, the lack of brain size reduction does not necessarily argue against Cieri's et al. (2014) model.

Considering all of the above, the role of the work by Cieri et al. (2014) can be considered as the foundation for a new field of research rather than an article aiming at presenting a definitive model or hypothesis. The authors did good on identifying certain domestication syndrome traits on the human species and discussing them within the perspective of selection for tameness/reduced aggression. Although their initially proposed mechanism for this type of selection was not promising, they shifted towards a more plausible one. However, it is worth mentioning that identification of a single factor or mechanism for such a process is most likely impossible, and that most surely several mechanisms would have driven selection against aggression (if given). Overall, the model proposed by Cieri et al. (2014) is consistent and of interest for the study of human evolution due to its integrative approach.

5.2 On human self-domestication after Cieri et al. (2014)

Following Cieri et al. (2014), Theofanopoulou et al. (2017) did one of the most relevant works regarding the human self-domesticaiton hypothesis. Theofanopoulou et al. (2017) found support for the human self-domestication hypothesis by finding overlap in genes under positive selection in humans and domesticates, being these overlapped genes related to neural crest development. This finding not only further supports the vision that the domestication syndrome common to all domesticates has its origin in shifts during neural crest development, but most importantly, finds evidence that these changes in neural crest development may also have occurred in humans, making Cieri's et al. (2014) model more consistent.

Evidencing the integrative approach of Cieri's et al. (2014) model, recent studies have embraced the human self-domestication hypothesis from the perspective of different fields. For instance, Burraco & Kempe (2018) discussed how the context set by the human self-domestication hypothesis (changes in brain cognition, increased social complexity) can provide an explanation for the origin of modern exoteric languages (this is, the ones allowing communication between different well-defined groups). Gleeson & Kushnick (2018) analysed the role of intersexual selection as a possible mechanism leading to human self-domestication, and their results regarded that intersexual selection may have taken place under certain cultural and environmental conditions. Wrangham (2018) argued that the fact humans are more prone to proactive aggression than to reactive aggression (which is something rare among primates) would point towards unique human ancestral adaptations, such as selection against reactive aggression by capital punishment in hunter-gatherer societies (capital punishment constitutes a way of proactive aggression). Bruner & Gleeson (2019) hypothesized that there may be overlap between cognitive abilities derived from human self-domestication and the ones derived from tool using, encouraging further research to be done in the topic.

All these studies proof the explanatory power the human self-domestication hypothesis provides for some of the unique modern human characteristics. However, I consider that the next major step that should be done within the hypothesis would be to identify the exact phenotypic traits that may have been produced by a domestication-like process in humans. This would prevent the hypothesis from becoming a possible explanation for all kind of recent human evolution unknowns. A possibility to advance in this direction would be to study the role of the genes observed by Theofanopoulou et al. (2017) to be under positive selection while linked to neural crest development, and the main physiological pathways linked to them.

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