SELF-DOMESTICATION AND HUMAN EVOLUTION

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SELF-DOMESTICATION AND HUMAN EVOLUTION

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Table of Contents

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Editorial: Self-Domestication and Human Evolution

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Editorial on the Research Topic

Self-Domestication and Human Evolution

The human self-domestication hypothesis, which traces back to Darwin himself, has experienced a recent resurgence in interest as an account for how modern human behaviors, morphology, and culture might have evolved. Although modern humans exhibit many shared features with other closely-related species, there is evidence of a distinct suite of derived physical, cognitive, and behavioral traits which are indicative of a domestication-like process. In order to understand the evolutionary path toward these distinct human traits, we need refined evolutionary models that provide mechanistic accounts for the multiple feedback loops that occur between cultural and biological evolutionary processes, whereby selection pressures for modern human traits, including language, may have affected cultural practice, which, in turn, created niches that impacted their biological evolution. With recent advances in the field, the present volume brings together an exciting range of theoretical perspectives that aspire to this goal.

The human self-domestication hypothesis builds on the finding that, compared to extant primates and extinct hominins, humans exhibit many of the distinctive morphological, behavioral, and cognitive features also observed in domesticated animals. At least in recent specimens, these include reduced skull/brain size, neotenic features, reduced sexual dimorphism, reduced reactive aggression, increased sociability, playfulness, social tolerance as well as enhanced sensibility to social and emotional cues (see Hare, 2017 for review; and Sánchez-Villagra and van Schaik, 2019 for a critical view). Although typically done in a pre-meditated way with domesticated animals, selection for more tolerant sexual and social partners (selection against aggression) has been hypothesized to have triggered a process in humans akin to domestication. Intriguingly, it has been suggested that a similar process may have also occurred in our closest ape relatives, the bonobos, who also show a similar trait of enhanced social tolerance, reduced aggression, and a suite of other neotenous traits (Hare et al., 2012). In *Homo*, features of self-domestication have been exacerbated in our recent history, reaching their peak during the Upper Paleolithic, when crucial changes in behavior, cognition and culture are thought to have occurred (Cieri et al., 2014). Selection against aggression has been argued to facilitate the creation of the special niche favoring the emergence of complex behaviors via cultural evolution. Accordingly, self-domestication has been invoked to account for key innovations in our behavior and cognition, including enhanced cooperation and complex social networks, cumulative culture, advanced technologies, and language (Hare et al., 2012; Hare, 2017; Thomas and Kirby, 2018; Benítez-Burraco and Progovac, 2020).

The main objective of this volume is to showcase some of the most recent accounts of the human self-domestication hypothesis. Such accounts require a more comprehensive characterization of humans as self-domesticates at the morphological, cognitive, or behavioral levels, as some domains are certainly underexplored. Accordingly, the contribution by Bruner and Gleeson considers the impact of self-domestication on brain-body-tool integration, i.e., the integration

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between brain morphology (particularly, the parietal cortex), cognitive function (specifically, visuospatial integration), and behavior (i.e., tool manufacture and use). These authors propose a feedback effect between the expansion of the parietal cortex driven by increased neural plasticity and sociability afforded by an extended juvenile period, and improved visuospatial cognition as a prerequisite for the ability to integrate tool-use with body schemas allowing humans to off-load cognition into complex cultural practices.

A second objective of the volume is to gain greater traction on what factors may have driven the emergence of domestication features in humans. Wrangham reviews proposals for potential human self-domestication mechanisms and concludes that language, specifically, "language-based conspiracies," acted as a driver of self-domestication by contributing to reduced reactive aggression allowing groups to unite in shared intentions of punishing aggressive individuals. A central role of language in the process of human self-domestication is also proposed in contributions by Murphy and Progovac and Benítez-Burraco. Murphy links self-domestication explicitly with models of language evolution whereas Progovac and Benítez-Burraco explore the more specific role of a feedback effect between reduced reactive aggression and improved verbal behavior as its replacement in the acceleration of human self-domestication, and advance several ideas about the nature of human languages during early Prehistory.

A third objective, addressed by four papers in this issue, is to improve our understanding of the effects of human self-domestication on the evolution of complex human social-cultural practices. Kessler explores the role of self-domestication in the emergence of human healthcare behaviors, conceived of as a merger of the capacity for social care for individuals that capitalized on human offspring care propensities, and community health behaviors which evolved independently in animals. Lenfesty and Morgan explore the interaction between prestige hierarchies that manifest themselves in religious practices and social learning of prosocial behaviors that may have contributed to self-domestication. Belfer-Cohen and Hovers present archaeological evidence relating self-domestication to the emergence of social cognition that promotes within vs. between-group categorization of conspecifics and serves as a driver of cultural evolution. Finally, Barron and Hare explore the contribution of self-domestication to the evolution and maintenance of human same-sex attraction. These authors suggest that same-sex sexual behavior reinforces enhanced prosocial tendencies such as social bonding, appeasement and play that result from, and contribute to, human self-domestication.

Finally, given an ongoing degree of controversy regarding the self-domestication hypothesis, a last objective of this volume is to present some critique and alternative accounts of human evolution. Shilton et al. identify contrasts between human social evolution and that of domesticated mammals, and conclude that rather than for reduced aggression, modern human evolution may have instead being driven by selection for socially-mediated emotional control and plasticity. This places a relevant note of caution to an approach that views human evolution exclusively as the outcome of a self-domestication process and, as a consequence, may inspire greater integration of different theoretical perspectives in future research.

Overall, this volume contributes a diverse collection of papers that tackle the exciting challenge of providing new views on human evolution which will ultimately help us to form a better understanding of the nature and the origins of human cognition, behavior, and culture.

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Body Cognition and Self-Domestication in Human Evolution

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DOMESTICATION AND HUMAN SELF-DOMESTICATION

The term “domestication syndrome” describes a range of correlated trait changes seen in domesticated populations when compared to their wild relatives or ancestors (Jensen, 2006; Wilkins et al., 2014; Zeder, 2015). Controlled experimental breeding has demonstrated rapid emergence of this syndrome in several mammal populations selected for dampened reactive aggression and stress response (Trut, 1999; Jensen, 2006; Kulikov et al., 2016). These results confirm findings of correlated change from longstanding observational research in domesticated lineages (Hemmer, 1990). Known traits include: docile behavior; reduced sexual dimorphism; reduced prognathism; smaller teeth; skeletal gracility; reduced brain sizes; altered oestrus cycles and fertility; floppy ears; elevated vocal communication; and altered pigmentation (Hemmer, 1990; Wilkins et al., 2014; Sánchez-Villagra et al., 2016; Okanoya, 2017). Many of these features are known to appear rapidly, as heterochronic shifts in ontogeny (i.e., paedomorphism or neoteny), rather than as isolated and adaptive mutations (Belyaev, 1979; Trut, 1999; Jensen, 2006; Zeder, 2012, 2015). Heritable hypoplasia of neural crest cell-derived tissues provides the most widely supported proximate explanation for these observed trait correlations (Wilkins et al., 2014).

Interestingly, several traits seen in bonobos (Hare et al., 2012) and in humans (Groves, 1999; Leach, 2003; Cieri et al., 2014; Thomas and Kirby, 2018) suggest intraspecific interactions can drive a process of “self-domestication” via socio-sexual selection for higher social tolerance and less reactive aggression (Cieri et al., 2014; Hare, 2017; Wrangham, 2018). In *Homo sapiens*, this process is thought to have enabled an expanded cooperative ability, leading to improved language and knowledge-sharing, thereby promoting social complexity and technological advancement (Hare, 2017; Thomas and Kirby, 2018). Humans are also characterized by an outstanding capacity for integration between brain, body and tools, and the evolution of this ability is associated with neuroanatomical changes of the visuospatial association cortex (Bruner, 2018). Whilst current scholarship is yet to address the potential for interaction between self-domestication and body cognition, we hypothesize that there may be value in an examination of any overlap. As such, here, we consider whether and to what extent these phenomena shared common evolutionary factors or reciprocal influences.

THE EVOLUTION OF THE PARIETAL CORTEX IN HUMANS

One of the main goals in evolutionary neurobiology is to identify features and aspects of the human brain that differ from other living and extinct primates (Preuss, 2017). When compared with extant taxa, *Homo sapiens* is characterized by cerebral features specific to our species, even if, for many of them, it is not clear whether they reflect simple differences in size (due to our peculiarly larger brain) or are entirely novel cerebral traits. Comparison with fossil hominids reveals differences in brain size, but a shared sulcal pattern and overall morphological organization (Bruner, 2017). Notably, there are differences in the cortical proportions of the parietal lobe, which shows dorsal regions that are wider in Neanderthals and generally much larger in modern humans (see Bruner, 2018 for a review). These regions spatially correspond to the precuneus and to the intraparietal sulcus, which have a larger and more complex cortical surface in humans when compared with other primates, including apes.

The parietal cortex is involved in multiple association tasks, but is particularly crucial for visuospatial integration—bridging body and vision, and coordinating eye and hand—and is central to functions like visual imaging, body-centered space and time simulation, and self-awareness (Fletcher et al., 1995; Cavanna and Trimble, 2006; Margulies et al., 2009; Freton et al., 2014; Land, 2014). These functions are also involved in relationships between brain and body and between body and environment; key factors that allow offloading and exporting of cognitive functions to external components (especially technology), thereby integrating tools into cognitive schemes of the body (Byrge et al., 2014; Bruner and Iriki, 2016).

Morphological changes in the modern human parietal cortex are not described among early *Homo sapiens* populations (say 100–300 thousand years ago), but are detected in later specimens, roughly at the time the archaeological record begins to show complex tools, projectile technology, and complex graphic culture (Bruner and Pearson, 2013; Neubauer et al., 2018). These developments, and this timeframe, have also been associated with reductions in masculine craniofacial morphology thought to indicate a process of human self-domestication (Cieri et al., 2014). If self-domestication was a crucial process in modern human evolution, and if body-tool extension and visual imaging have been key factors in modern human parietal cortex development, it makes sense to expect some interaction between their relative causes, effects, and functional mechanisms. As such, it appears worthwhile to consider whether these two features (self-domestication and visuospatial cognition) exert reciprocal influences and, further, whether these complex processes may share contributing factors in common (**Figure 1**).

THE DOMESTICATED BRAIN

In general, brain size is substantially reduced in domesticated lineages when compared to non-domesticated forms (Kruska, 1988, 2005), and such reduction is more prominently expressed in more encephalized taxa (Kruska, 1988). Brain size reduction should, therefore, be particularly apparent in modern humans under the effects of domestication. However, although late modern humans display smaller cranial capacity when compared with earlier populations (Henneberg, 1988; McHenry, 1994; Ruff et al., 1997), relative brain size appears to have increased, because of a simultaneous reduction of body size (McHenry, 1994). We can wonder whether the novel expansion of derived areas (like the parietal ones) could have partially contrasted and masked a generalized reduction of brain volume in our species.

During domestication, limbic structures are particularly reduced (Kruska, 1988). This is probably crucial to achieve a lower aggressive reactivity and, accordingly, to promote and extend social bonds. However, presently available evidence suggests that humans have relatively larger—instead of smaller—limbic components (hippocampus, amygdala and orbito-frontal cortex), at least when compared with living apes (Barger et al., 2014). Such structures are, unfortunately, not directly detectable in fossil species, or in early modern humans.

JUVENILE BRAINS, BODIES, AND TOOLS

Many non-human species utilize “objects” to some extent, but only humans use “tools,” as defined in a strict sense. Here, we suggest that to be “a tool,” an object must fulfill at least three crucial conditions. First, it must be integrated within the body schemes of the brain, as a real extension of its space and functions (Maravita and Iriki, 2004; Tunik et al., 2007; Heed et al., 2015). Second, it must be part of a productive chain, in which a propaedeutic sequence of tools is necessary to achieve a final target (Muller et al., 2017). Third, it must not simply *assist* the ecological and economical behavior of a species, but must be *integrated-with*, and *necessary-to*, a cultural niche (Plummer, 2004). Humans achieve these three conditions by integrating technology into cognitive processes, literally as a spider does with its silk web (Kaplan, 2012; Japyassú and Laland, 2017). According to theories in extended cognition, tools are proper functional elements of our cognitive system (Malafouris, 2010, 2013). That is, our cognitive process does not rely only on the neural system, but also on extra-neural components (technology) to which we delegate specific cognitive functions (Overmann, 2015). Such *prosthetic capacity* can be defined as the capacity to delegate cognitive functions to external elements, offloading and outsourcing information processing to peripheral (out-of-the-body) components. The parietal cortex in humans is involved in tool use and tool making (Grefkes and Fink, 2005; Bzdok et al., 2015; Goldring and Krubitzer, 2017; Kastner et al., 2017), and hence particularly involved in body-tool extension and integration (Bruner and Iriki, 2016). Human prosthetic capacity is largely enhanced by the remarkable plasticity of our cortical system (Sherwood and Gómez-Robles, 2017), and by the high level of creativity and explorative innovation of our species (Kyriacou and Bruner, 2011). Both features (neural plasticity and explorative behavior) are primarily associated with juvenile life stages and have been enhanced by extension of the juvenile period in humans (Bogin, 1990; Pellegrini et al., 2007). Given that animal domestication is broadly associated with a trend toward relative juvenilization (Harvey and Clutton-Brock, 1985; Smith, 1992; Joffe, 1997), aspects of human self-domestication may also contribute to our enhanced technological capacity. In fact, altered timing and stretching of the life-history is implicated in the extension of those ontogenetic stages more sensitive to novelty, the extension of the post-reproductive period, and the extension of life in general (longevity). All of these aspects of human

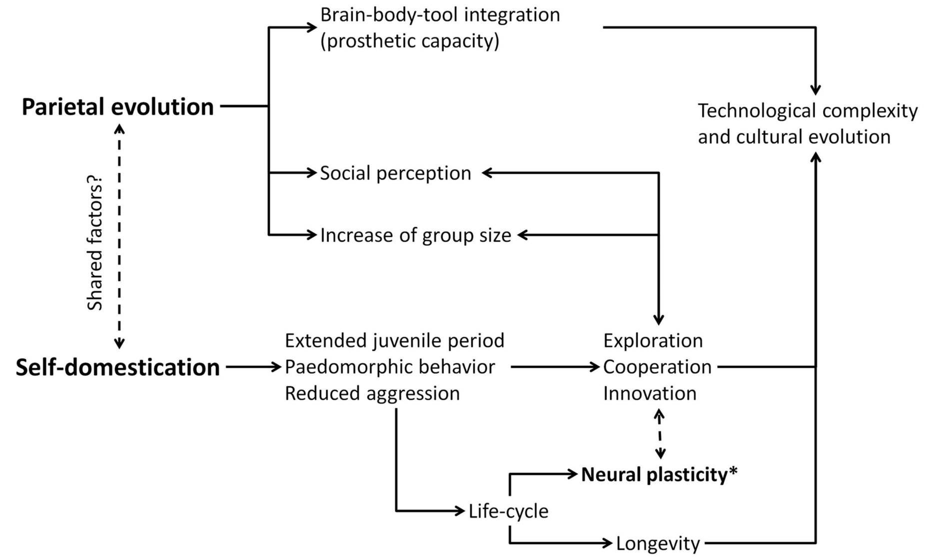

FIGURE 1 | Diagram of possible relationships between parietal evolution and self-domestication. Neural plasticity (*) can be a key factor, being targeted by selective processes as to enhance cognitive, cultural, and social capacities.

life-history are strictly necessary to generate intergenerational transfer and cultural evolution (Kaplan and Robson, 2002; Lee, 2003), providing a further link between self-domestication and technological extension.

Interestingly, interpreting parietal expansion as an evolutionary novelty may complicate one diagnostic feature of the supposed juvenilization process in humans: that is, the roundedness of our head, which is often explained as a pedomorphic feature, but which could actually represent an apomorphic cortical character, mimicking a juvenile appearance. Apart from parietal bulging, vault globularity in our species is also due to the curvature of the frontal squama, likely to be a secondary structural consequence of having a reduced facial block positioned under the frontal lobes (Pereira-Pedro et al., 2017). This latter feature can indeed be associated with a pedomorphic process, at least if we consider the reduction of the splanchnocranium as a juvenile heterochronic retention.

ASSOCIATION CORTEX, BODY PERCEPTION, AND SOCIAL EVOLUTION

A further potential locus of association between parietal expansion and self-domestication is increased sociability. The experimentally demonstrated proximate cause of domestication syndrome is selection against reactive, or autonomic, aggressive response (Trut, 1999; Jensen, 2006; Wilkins et al., 2014). This selective mechanism is thought to have facilitated the emergence of language, increased group sizes, and elevated cooperation in humans (Cieri et al., 2014; Hare, 2017; Thomas and Kirby, 2018). In primate species, group size is proportional to brain size and, for humans, it approaches 150 units (i.e., "Dunbar's number"—Dunbar, 2012, 2018). Interestingly, this correlation particularly concerns the association cortex, probably because of a direct relationship with behavioral complexity (Dunbar and Shultz, 2007; Pearce et al., 2013). The parietal cortex is one of the main association regions (Krienen and Buckner, 2017; Mars et al., 2017) and, in this case, its expansion is likely to have a direct effect of social group size. Moreover, the parietal cortex and visuospatial integration are involved in self-recognition, self-other perception, body-centered simulation, and in the management of a "social space" which uses the body as a functional and metric unit (Hills et al., 2015; Maister et al., 2015; Peer et al., 2015). Actually, the precuneus has been hypothesized to be a crucial element of the network involved in mind reading (Heyes and Frith, 2014). These features (increased social group size through increase of association functions, and the capacity to handle a social space based around one's own body) are strictly intermingled with social effects expected from self-domestication and associated juvenilization, namely an increase in the size and complexity of the social network.

CONCLUSIONS

We hypothesize that, in humans, changes associated with self-domestication might have influenced, or been influenced by, body cognition, visuospatial integration, technological extension, and the evolution of the parietal cortex. Alternatively, these features may be independent, and might have evolved independently along the human lineage. These two hypotheses should be discussed and evaluated according to a comparative and functional perspective by investigating this possible association in other primates and considering the corresponding relationships between anatomy, development and cognition. Some aspects of these evolutionary features are likely to have interacted, generating reciprocal enhancement. Others may hide common mechanisms, possibly due to ontogenetic communalities and shared developmental components. In this regard, one candidate may be neural plasticity, which is both a crucial consequence of paedomorphic conditions and a feature particularly influencing the development of the parietal cortex because of its sensitivity to sensorial (somatic and visual) inputs. We can wonder whether sociability associated with self-domestication, an extended juvenile period, and increased neural plasticity, could have prompted the expansion of the parietal cortical surface, subsequently triggering retroactive feedback to enhance its functional consequences. Association cortices may be the result of multiple crossing gradients between sensorimotor regions, generating a patchwork of neural combinations in terms of functional properties (Huntenburg et al., 2017). In this case, prolonged or increased plasticity of the body-vision system may be the essential prerequisite for developing a more anatomically and functionally complex prosthetic capacity, as the ability to incorporate tools into body schemes, offloading cognitive processes to external elements. Importantly, it remains to be evaluated whether this process is strictly associated with the evolution of modern humans (*Homo sapiens*), or can be traced back to the origin of our genus. In any case, it seems important to consider these processes and functions together when attempting to determine a comprehensive evolutionary narrative for our species.

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Both authors have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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REVIEW
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No Country for Oldowan Men: Emerging Factors in Language Evolution

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Language evolution has long been researched. I will review a number of broad, emerging research directions which arguably have the potential to contribute to our understanding of language evolution. Emerging topics in genomics and neurolinguistics are explored, and human-specific levels of braincase globularity – and the broader process of self-domestication within which globularity seems capable of being encapsulated – will be argued to be the central pillars of any satisfactory and interdisciplinary model of language evolution.

Keywords: domestication syndrome, molecular clock, genetic drift, globularity, language evolution, basicranial angle, birdsong

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INTRODUCTION

In recent years, a number of models have been proposed to explain the implementational basis of hierarchical phrase structures (reviewed in Aboitiz, 2017; Friederici, 2017). A range of paleoanthropological, paleoneurological and genetic data has also been consulted in an effort to map out an accurate path that language evolution likely took (Zollikofer and Ponce de León, 2013; Benítez-Burraco and Boeckx, 2015; Beaudet, 2017; Murphy and Benítez-Burraco, 2018a,b). My intention here is to review some possible connections between these distinct modes of inquiry by exploring a specific set of phenotypic traits and evolutionary processes which have the potential to explain the emergence of core features of language such as syntactic complexity and unrestricted semantic combinatorics.

This review will begin by focusing on genetics ("Gene Regulation," "Genetic Drift," "Comparative Genomics," "Molecular Clock," and "DNA Sequencing") and then progress to broader evolutionary themes ("Globularity," "Tool Use") and emerging directions ("Domestication," "The Cerebellum and Speech").

GENE REGULATION

Beginning with the genetic foundation of a possible model of language evolution, we can consider what the likely *mutational profile* of its initial stages were. It has been proposed that there exist 1,241 primate-specific genes (Zhang et al., 2011), 280 of which are human-specific. Fifty-four percent of these human-specific genes are upregulated in a brain area implicated in higher cognition, the prefrontal cortex. These new genes are significantly more likely to be involved in gene regulation (Diller and Cann, 2013, p. 256), although, as we will see below, exploring the genetic basis of other brain regions will also be required to account for language evolution. The mutation of some regulatory gene may have reorganized the neuronal populations in the neocortex and its concomitant computational properties (although the precise nature of these neurolinguistic properties is beyond the scope of this general review; see Friederici, 2017). Given the level of regulatory complexity identified by Chakravarti (2011) – "compromising the activity of one gene need not cripple an entire network"; "variation in the regulatory machinery of genes is much more frequent than that in the structure of gene products" – it is more likely that the neurocomputational properties required for language emerged after the mutation of multiple regulatory genes acting in concert, and not a singular mutational event as often claimed in the generative and biolinguistics literature (e.g., Chomsky, 2010): "Genes and their products almost never act alone, but in networks with other genes and proteins and in [the] context of the environment" (Chakravarti, 2011, p. 15).

Is there any indication that this general picture is reasonable? Consider how the transition from the many digits of lobe-finned tetrapods to only 5 was not the result of new genes, but rather of distinct regulations of existing genes, namely regulation of *Hoxa11* (Kherdjemil et al., 2016). A similar account may be applied to core features of language, in particular given that there exists no strong correlation between the total number of genes in a given species and the level of biological complexity it achieves (for instance, mice and humans have comparable numbers). Of relevance here is the finding that human evolution has slowed down, often called the "hominoid slowdown": "[R]ates of occurrence of *de novo* mutations decreased as enhanced DNA repair mechanisms and larger generation times evolved" (Goodman, 1985, p. 10). Hominoids appear to have reached a certain mesa of complexity, with only slight tuning yielding novel benefits.

In summary, a slight regulatory change could have produced an alteration in the human computational system yielding the capacity for constructing hierarchical phrase structures.

A separate question now concerns when this took place. Putting aside precise dates, and assuming that anatomically modern humans emerged around 300–150 kya (kya: 1000 years ago), it appears that the vast majority of complex forms of symbolic representation did not emerge until 100–60 kya (Hurford, 2011). We will present a more detailed timeline below after considering a broader range of topics, but for now we can note that this time also correlates with the emergence of new migration patterns (Mellars, 2006), leading to the possibility that properties of the environment acted as release factors for language. Encountering new forms of social organization and environments may have served to prompt the basic combinatorics of mammalian cognition and encourage novel forms of conceptual combination. Bolender (2007) has suggested along these lines that an increased human population, leading to a greater complexity of inter-group communication, acted as a trigger for the use of syntactic word movement, hitherto dormant. If this is correct, then investigating syntactic phenomena from a purely computational perspective, not considering the influence of the development and emergence of the phenotype, would be missing a crucial part of any psychological or cognitive account.

GENETIC DRIFT

We can now turn to a related topic, which has become just as controversial in the language evolution literature. One of the most general distinctions in this literature is between theories that assume language emerged suddenly, and theories that assume it emerged gradually. What does the archeological record have to say about this? Unfortunately, since the African middle Pleistocene hominin record is sparse, it is currently not possible to determine whether fossils like Omo Kibish 1 mark the earliest forms of the constellation of human features or whether older types exist. Another major question concerns whether human features emerged through natural selection or through random *genetic drift*. This occurs when the proportion of a gene variant in a population changes due to external events ("chance"). Coyne (2009, p. 14) notes that "genetic drift may play some evolutionary role in small populations and probably accounts for some non-adaptive features of DNA." Examining cranial measurements, Weaver et al. (2008) show that the differences between Neanderthals and anatomically modern humans could have emerged under drift over a period of around 400,000 years. Moreover, Weaver and Stringer (2015) show that these cranial differences emerged in a highly unconstrained way thanks to cultural buffering, relative to morphological divergences documented between crania of subspecies of *Pan troglodytes*.

While it is well known that only ∼4% of the human genome differs at the nucleotide level from the chimpanzee genome (Varki and Altheide, 2005), the way that these genes are expressed is far from uniform. For instance, there is up to an 8% difference in splicing rates in the cortex between humans and chimpanzees (Calarco et al., 2007), with NDE1 (a gene involved in cortical neurogenesis) recently being shown to exhibit human-specific splicing patterns. Splicing consequently seems to be a major mechanism of brain evolution and cognitive development (Mosca et al., 2017).

COMPARATIVE GENOMICS

Comparative genomics yields other fruitful insights into the likely origins of language. Gronau et al. (2011) analyzed the whole-genome variation diversity patterns of six people from contemporary sub-populations: European, Yoruban, Han Chinese, Korean, Bantu, and San African. The final group (speakers of Khoisan) were discovered to have likely split from the rest of the human population around 157–108 kya, and since they possess the ability to acquire language this indicates a likely timeline. Behar et al. (2008) report that mitochondrial DNA (mtDNA, transmitted through maternal inheritance) in the Khoisan peoples diverged from mtDNA in the human gene pool as early as 160 kya years ago, remaining separate until around 40 kya. The genetic isolation of the San people matches with the isolation of a core part of their language use. All Khoisan groups use clicks; Moisik and Dediu (2017) use a biomechanical model to show that a reduced alveolar ridge aids the production of clicks, and that this has been selected for amongst Khoisan groups. Clicks are complex obstruents externalized via a double closure in the oral cavity. Huybregts (2017) notes the intriguing possibility which follows from these findings. The common human population shared by the San and the rest of contemporary human societies must have had language but may not have solved the problem of externalization, i.e., they may have exhibited the ability to recursively construct hierarchical representations, but not the ability to map this capacity to the sensorimotor system for externalization via speech, gesture, and so forth. The San population and the non-San populations therefore solved the problem in different ways, indicating a clear timeline: the computational system of language evolved before it was linked to externalization.

Nielsen et al. (2017) also discuss how "genetic markers with uniparental inheritance and linguistic studies suggest that click-language-speaking hunter-gatherer populations may originally have been more widespread and were replaced in areas other than southern Africa or, alternatively, that they may have originated in eastern Africa and then migrated to southern Africa in the past 50 kyr." Furthermore, "other hunter-gatherer populations that speak languages that use clicks, including the Hadza people and the Sandawe people, currently reside in Tanzania in eastern Africa, although they display limited genomic affinity with the San people of southern African."

Lastly, despite the question of modern human origins in Africa remaining unsettled, a multiregional origin in which modern (domesticated) features evolved in a fragmented way in multiple areas connected by gene flow is a strong possibility. There is evidence, for instance, for the admixture of modern humans with archaic populations in Africa (Hammer et al., 2011). Statistical analyses of whole-genome sequencing data from geographically diverse hunter-gatherer populations also presents evidence of archaic human lineages that underwent introgression (i.e., exchanging genetic material via interbreeding) and diverged from modern human lineages anywhere between 1.3 mya and 35 kya, and so the extent of archaic admixture remains a point of controversy: "Perhaps of greatest interest is genomic data from under-sampled regions of the world, which may help to refine evolutionary theories, including the question of whether there are further, as-yet uncharacterized, lineages of archaic humans" (Nielsen et al., 2017, p. 308).

MOLECULAR CLOCK

Another topic which I would like to argue is relevant for language evolution research is the *molecular clock*, in particular given that many core hypotheses about the origin of recursive hierarchical phrase structure concern sudden and chance mutations. In recent research, the speed of the molecular clock has been calculated in terms of the number of mutational differences in matching segments of DNA between humans and primates based on the fossil record. Because it has typically been assumed that the speed was high, the "Out of Africa" migration was thought to have occurred around 70 kya (e.g., Gibbons, 2012). More recently, however, a new method of obtaining mutation rates has emerged which calculates the rate of the full genome of present-day humans through counting the number of new mutations in the nuclear DNA of a newborn compared to its parents. Scally and Durbin (2012) cite the value at 0.5×10^{-9} bp^{-1} year^{-1}, which is around half of the previous fossil-calibrated rate (Ike-uchi, 2016).

As such, the molecular clock is much slower than previously believed. Adjusting for these new calculations, the migration from Africa is likely to have occurred around 130 kya (Ike-uchi, 2016) (as the fossil record also suggests).

A possible scenario for language evolution in line with these findings is that the mutation(s) required for language occurred in an individual between 200 and 130 kya in East Africa. This then spread through the community, and around 130 kya a group (composed of around ∼450 individuals, according to estimates in Fagundes et al., 2007) migrated north across Arabia, passing the Bab al-Mandab Straits and progressing to Oman and the surrounding regions, eventually arriving in southern China and Indo-China. A separate group, much later (100–50 kya) also left North Africa through a different route (the Nile Valley) and reached Eurasia. Of course, the hypothesis that a small number of mutations in a relatively short time window led to language is naturally compatible with whatever theory one adopts concerning the speed (fast or slow) of the molecular clock. But the notion of a slow clock nevertheless makes the standard generative picture of a *sudden, slight mutation* somewhat less appealing, and rather points to the validity of a series of mutations. None of these discrete changes would have likely been sufficient to bring about the morphological and neurological characteristics of the anatomically modern human brain, but when spread throughout a community for extended periods they may have conspired to do so.

DNA SEQUENCING

Having covered some broad topics in genomics, what can be said about the emerging theme of technological advances with potential to inform models of language evolution? Developments in DNA sequencing recently resulted in sequence data covering much of the Neanderthal genome (Green et al., 2010). Shortly thereafter, a list of 87 genes with protein-coding differences between humans and Neanderthals was released (Prüfer et al., 2014). This allows hypotheses to be drawn up concerning the existence of certain language-relevant cognitive components in Neanderthals. The most famous (and notorious) candidate for a "language gene" is *FOXP2*. This codes for a transcription factor (a protein able to bind DNA and modify the expression of other genes) connected to a large network of genes that can be up- or down-regulated (Vernes et al., 2007). In modern humans the gene exists in a species-specific allele, coding a protein differing from that of chimpanzees (Enard et al., 2002). *FOXP2* currently seems to have no variation that might have distinguished Neanderthals/Denisovans from humans. But as DeSalle and Tattersall (2017) note, this is an extremely weak basis from which to claim that Neanderthals/Denisovans had language. Prüfer et al. (2014) drew up a list of candidates for the Neanderthal genome and, as DeSalle and Tattersall (2017, p. 5) comment, these authors "do not appear to have made any strong connections between language and any of the genes they determined as important in the differentiation of the Neanderthal/Denisovan genomes." Of all the candidate genes for language summated via extensive review by DeSalle and Tattersall (2017), only one has a serious and promising connection to the Prüfer et al. (2014) database: CNTNAP2. This plays an important role in nervous system development and covers 1.5% of chromosome 7, although it currently remains unclear how it could causally relate to language evolution (see Mountford and Newbury, 2018 for further discussion). A regulatory region of FOXP2 was recently identified exclusively in modern humans at a binding site of the transcription factor POU3F2 (Maricic et al., 2013). This documented POU3F2 change that enhanced FOXP2 expression in the human brain was also not part of the gene flow from humans into Neanderthals that occurred in the Levant or Southern Arabia 125–100 kya (Kuhlwilm et al., 2016). Since this likely resulted in improved speech, it is not unreasonable to associate linguistic externalization with this POU3F2 haplotype at FOXP2, suggesting that externalization was a late development occurring after the initial computational system had emerged. This research suggests that "differences in gene regulation and expression may be involved in cognitive function, and that species differences are due to far more than just two variants in a single gene" (Mountford and Newbury, 2018, p. 55).

Building on these developments, Murphy and Benítez-Burraco (2018b) argue that since we cannot track the neuronal activity of the brain from extinct hominins, it is reasonable to use our current understanding of the language "oscillogenome" (that is, the set of genes responsible for basic aspects of oscillatory brain activity relevant for language; see Murphy and Benítez-Burraco, 2018a) to infer some properties of the Neanderthal oscillatory profile. Several candidates for the language oscillogenome show differences in their methylation patterns between Neanderthals and humans, and Murphy and Benítez-Burraco (2018b) claim that differences in their expression levels could be informative of differences in cognitive functions important for language (e.g., working memory).

Exploring a broad topic such as the genetics of language will require a number of linking hypotheses between genes, neural anatomy and cognitive processes. Without such linking hypotheses, it becomes extremely difficult to draw any substantial conclusions about the genetic foundations of language. For instance, the gene *SRGAP2* has often been invoked in discussions of language since it has been shown to be involved in cortical growth (Hillert, 2015). The occurrence of certain hominins correlates with copies of the genes, but also with the appearance of different artifacts, and so it is difficult to even generate any inferences let alone adjudicate between different hypotheses.

More broadly, Fisher (2013) makes the crucial point that genes do not specify behavioral outputs, and do not even code for specific cognitive "modules." Rather, gene products (usually proteins) interact with one another in complex networks to construct neural circuitry through modulating neuronal proliferation and migration, neurite outgrowth, axon pathfinding, synaptic strength, and so forth. Most genes, in particular regulatory genes, play multiple roles within an organism ("pleiotropy"). In short, genes do not code for "language" or "speech," and an individual gene is rarely expressed in only one part of the central nervous system, with *FOXP2*, for instance, being expressed in the cortex, basal ganglia, thalamus and cerebellum (Lai et al., 2003).

GLOBULARITY

Pushing our timeline back even further now, the human lineage began around 6 mya, when our common ancestor with chimpanzees split into separate lineages. Likely the closest we have to a last common ancestor was *Ardipithecus*, who lived in trees but was capable of bipedalism. Standing at 4 feet tall, their brains are estimated to have been at around 500 cubic centimeters. The oldest fossils ascribed to the genus *Homo* (emerging around 2.5 mya) are from Kenya, Ethiopia, Tanzania, and South Africa, and include cranial and postcranial specimens. These are classified as *Homo erectus*. While there is some controversy about the earliest suggestive evidence of *Homo* in species such as *Homo habilis*, *Homo naledi*, and *H. erectus* (a fragmentary upper jaw with a partial dentition from Ethiopia, dated at 2.33 mya), these cranial and postcranial specimens are the earliest fossils we can ascribe with confidence.

Skulls of subsequent members of *Homo* exhibit an increasingly high and globular morphology, forming the marked parietal bone eminences of anatomically modern humans. With respect to the development of the posterior inferior frontal gyrus, the general trend throughout hominin evolution appears to be a reduction in size on the left relative to the right, while the region more broadly projects more laterally and antero-posteriorly on the right side. Consequently, left Broca's area appears more globular (Balzeau et al., 2014). Recent re-evaluations of the fossil record have revealed a more complex picture of frontal lobe evolution than is typically assumed, such that the inferior frontal gyrus and Broca's cap have indeed assumed a more globular shape (in line with the rest of the forebrain more generally), i.e., they have assumed a rounder shape as opposed to a flatter projection across the cortex (Beaudet, 2017).

Building on these concerns of globularity, a recent review of 20 *Homo sapiens* endocasts from different time periods employing computed tomographic scans and geometric morphometric analyses was conducted by Neubauer et al. (2018). Endocasts approximate outer brain morphology very closely due to the fact that the brain, meninges and cranial bones interact during development. The authors showed that while modern human brain size was assumed as early as 300 kya (hominin fossils from Jebel Irhoud, Morocco), it was not until 130–35 kya that our modern, globularised brain shape emerged (that is to say, the Jebel Irhoud fossils were not globular). Crucially, Neubauer et al. (2018) note that this process "paralleled the emergence of behavioral modernity as seen from the archeological record." They add that "the 'human revolution' just marks the point in time when gradual changes reach full modern behavior and morphology and does not represent a rapid evolutionary event related to only one important genetic change" (see also Murphy, 2018 for a proposal that this process of globularisation granted "traveling" neural oscillations the ability to migrate across new areas of the cortex and subcortex).

This suggests that while the capacity for constructing hierarchically organized linguistic structures (or phrase structure building) was available before the final stages of globularisation, these documented changes in brain shape (and their concomitant neural re-wiring) likely allowed this computational system to gradually interface with other previously encapsulated cognitive systems, due to this re-shaping reducing the number of "spatial inequalities" (Salami et al., 2003) in the brain, and hence the number of possible cross-regional connections. The phrase structure capacity may have emerged first, but also may not have achieved its full, modern reach until globularisation occurred. This suggests that language-music, language-mathematics and language-morality interfaces (assuming a common computational link between these capacities, à la Hauser and Watumull, 2017) emerged at different evolutionary timepoints and that it may be possible to plot a timeline for the emergence of these interfaces. For instance, we can date musical instruments to around 35 kya (such as bone and ivory flutes; Conard et al., 2009). In terms of their neuroanatomy, mathematical knowledge and language appear to involve distinct cortical networks (Amalric and Dehaene, 2019).

Additionally, no CT data of the Herto skull (160 kya) is available, and so it is possible that modern human-like globularisation was found as early as 160 kya, possibly before. If this is the case, then a more saltationist model of language evolution may be accurate such that language interfaced with other cognitive systems rapidly. Regardless, what can be said with certainty is that modern humans exhibit a more acute basicranial angle than other Great Apes, achieving a much more extreme level of globularity.

Turning to the related theme of neurolinguistics, neuronal networks have been shown to obey Rent's rule (a "third factor" in language evolution), a rule from computing logic, exhibiting hierarchical modularity that optimizes a trade-off between physical cost and topological complexity, such that these networks are cost-efficiently wired. Rent's rule states that the following relationship exists between several chip parameters.

$$T = AK^P$$

where T is the number of terminals, K the number of blocks within the chip, A the average number of terminals for one block, and ^{P} the Rent exponent. As Sengupta et al. (2013) summarize: "A modular design balances the savings in metabolic costs, while preserving computational capacities." A more globular braincase hosting a "folded" brain (which, through gyrification, permits a large surface area to fit inside a smaller skull), in conjunction with Rent's rule, maximizes computational efficiency and large-scale circuit integration. The implications for cognitive evolution may be substantial.

Although these empirical discoveries are novel, the general themes supporting them remain classical. Ever since Broca (1861) and Dax (1863), human brain asymmetries have been documented, often being used to help distinguish between different species. However, the oft-discussed process of lateralisation is "probably shared by all hominins" (Balzeau et al., 2014, p. 126), and so some other neural changes may have likely been responsible for language evolution. Consider Australopithecines, who comprise the human clade along with the extant genus *Homo*. These are assumed to lack the diverse behavioral and biological features exhibited by *Homo*, though the fossil record is far from complete. The oldest stone tools have been dated to around 2.6 mya, close to the likely appearance of the first *Homo*. This had led some to speculate whether the larger brains associated with early *Homo* specimens were required for the conceptualisation involved in using this type of tool (see Mann, 2011). Indeed, throughout the evolution of *Homo* brain size has almost tripled in volume. The earliest *Homo* had a braincase volume of 510–775 cc, whereas modern *H. sapiens* exhibit braincases with volumes ranging from 1200 cc to over 1500 cc. Influences of changing climate, environmental demands, and social competition are thought to be the major influences driving brain size change (Bailey and Geary, 2009). Although the trend toward brain size increase has been well documented in hominin evolution (Sousa and Wood, 2007), there are some important exceptions such as *Homo floresiensis* (Kubo et al., 2013) and the size reduction in *H. sapiens* since the Upper Paleolithic (Balzeau et al., 2014), a period lasting from 40 to 12 kya.

TOOL USE

Another domain with implications for language evolution, and one which has long been seen as relevant not just to linguistics but cognitive science more generally, is tool use. Archeologists studying the Paleolithic period have discovered the types of technology created by *Homo*. One such technology is composed of three types of basic stone tools: hammers, cores, and flakes. These are termed Oldowan tools, or Mode 1. These tools display substantial spatio-temporal uniformity with few modifications for more than 1 million years. Hominins used Mode 1 tools to kill and butcher medium- and large-sized mammals. Stone tools were also used to access bone marrow, and the surfaces of certain tools suggest that roots might also have been pounded (Wrangham, 2009). Upon the emergence of *H. erectus*, Acheulean tools (Mode 2) emerged, which were effectively enhanced versions of Mode 1 tools with the addition of a "biface"; namely, the margins of the tools were trimmed to either produce symmetrically sharp sides (as in the Acheulean hand ax) or a modified side meeting an unmodified side (as in cleavers). Acheulean tools were used to slice open animal skins, carve meat and break bones. Two examples of cutting tools typical of early Acheulean sites are pointed hand axes and picks, involving intentional shaping. Moreover, the intentional procurement of raw materials and the development of a multicomponent quarrying process was required to produce these tools. Mode 1 tools had no existence outside their conditions of use, but Mode 2 acquired a somewhat more abstract function. *H. erectus* carried them around, using them for distinct purposes and to achieve different goals, participating in the cultural life of the species. In this sense they acquired a symbolic, memetic existence, and they also naturally helped *H. erectus* consume the necessary amounts of meat needed to fuel its enlarged brain.

Indeed, it has often been suggested that because remains of one-million-year old campfires have been discovered and are thought to have been constructed by *H. erectus*, the invention of cooking might have provided a new range of nutrients feeding brain growth in *Homo* (Aboitiz, 2017, p. 452). DeCasien et al. (2017) provide novel statistical techniques to demonstrate that primate brain size is predicted by diet, not by degree of sociality, suggesting that studies of language evolution could benefit from a shift of attention toward ecological factors. The enlarged brain, in turn, seems to have been capable of coordinating spatial representations with shape recognition, necessary requirements for a biface; a process demanding an enlarged working memory for *H. erectus* relative to earlier *Homo* (Gibson, 1993). After these advances in mentally manipulating three-dimensional Euclidean space, it is not at all clear whether substantial advances in spatial cognition were made until the present, or whether the spatial reasoning skills of modern humans are closely comparable to those of *H. erectus*. One of the less controversial topics in human evolution involves the usefulness of dietary changes in providing the necessary nutrients and energy for sustaining hominin brain enlargement in early *Homo*. The modern human adult brain uses 20% of the body's metabolic energy, whereas new-borns use around 60% (Aiello et al., 2001), with growing brains needing a substantial range of foods (captured via sophisticated hunting tools) with high nutrient density. It is possible that these dietary (and, hence, social) changes had a selectional impact on certain aspects of speech or babbling (DeCasien et al., 2017).

Turning to Neanderthals, this species has always suffered from something of an image problem: In the early 20th century, the discovery of a Neanderthal skeleton from La Chapelle-aux-Saints in France exposed deformities which were at the time thought to be indicative of their cognitive and cultural degeneracy, yet it is now known that these were simply a reflection of the old age of the particular individual. The Neanderthals in Eurasia were a population whose lineage split from that of *H. sapiens* around 500 kya, and who disappear from archeological history around 30 kya. They exhibited use of Mode 3 tools, namely Mode 2 tools with "flake technology," producing intricate grooves along the sides of objects (surpassed only by Mode 4, or Solutrean tools; thin, sharp blades used by modern *H. sapiens*). They also introduced hafting of stone points onto spears, and lived in small communities, enjoying little to no contact with other Neanderthal groups outside local territory. Neanderthal remains have been found across Europe, and consequently play a major role in discussions of human evolution given that both species appear to have trekked out of Africa. Relative to modern humans, Neanderthals possessed a low, flat braincase, sloping foreheads and large brow ridges. Their brains were slightly larger than those of humans. Their chests were barrel-like, indicating "a body morphology adapted to the cold conditions of ice age Europe" (Mann, 2011, p. 279). Different Neanderthal groups exhibited distinctive features: "Fossil finds in northern Israel, such as those from the Tabun and Amud caves and the skeleton lacking a skull from the Kebara cave . . . possess features similar to other Israeli specimens, the Qafzeh and Skhul samples, which have been termed early modern humans" (Mann, 2011, p. 280).

Neanderthals also appear to have been capable of pyrotechnology. Early Neanderthals from the late Middle Pleistocene site of Poggetti Vecchi, Italy, seem able to have appropriately selected timber to create "digging sticks" (Aranguren et al., 2018; see also Hoffecker, 2018 for a review of Neanderthal technology). Kibblewhite et al. (2015) even propose a predictive framework for the preservation of materials (including bones, teeth, metals and organic materials) in soil across the European Union based on the chemical properties of discovered materials and the soil they were found in, allowing them to predict the most likely "hot spots" for future discoveries relevant for cultural/cognitive research.

Moving forward to the time of modern *H. sapiens*, the stone tools found at the Nubian Complex in the Dhofar region of Oman have been dated at 106 kya (Rose et al., 2011), providing evidence for the existence of a northeast African Middle Stone Age technocomplex exhibiting the Levallois technique of stone knapping, a complex method involving the extraction of a small plane from a larger surface. Humans may well have been responsible for this, and if so they likely left Africa as early as 110 kya.

However, Armitage et al. (2011) document how Levallois assemblages from Jebel Faya in the United Arab Emirates share close affinities with late Middle Stone Age assemblages from North East Africa. The authors date these Jebel Faya assemblages to 125 kya, pushing the migration out of Africa even further back to around 130 kya. In addition, the Lunadong hominin fossils discovered at Luna Cave in Guangxi, southern China, include one left upper second molar (M2) and one right lower second molar (m2). Bae et al. (2014) note that M2 is exclusively assigned to modern humans, while m2 is also likely to be. The teeth are dated between 127 and 70 kya, in turn suggesting an early migration from Africa and Arabia. Bae et al. (2017) review recent results from hominin paleontology, geochronology and genetics, concluding that there must have been multiple dispersals from Africa into Eurasia, rather than a single exodus.

In summary, we can say with some confidence that the apparently human-unique capacity for language-specific syntax emerged within the last 200 kya, and we can say this thanks to the development of sophisticated tools, cultural artifacts, complex trading relationships, and paintings. Indeed Miyagawa et al. (2018) draw a connection between cave paintings and "archeoacoustics," noting that cave art is typically connected to the acoustic properties of the chambers they are located in. Being sensitive to the echoes generated in these chambers, Miyagawa et al. speculate that cave paintings may have been a form of cross-modality information transfer through which acoustic signals are transformed into visual representations. Although we will likely never know whether these complex cave paintings demanded the existence of language to produce, they are nevertheless part of a wider movement in cultural flourishing which are indicative of substantial cognitive advances.

Given the hunter-gatherer culture in which this capacity emerged, what can we say of the "first words" (or units of semantic communication) which would have been externalized? Naturally we can only speculate, but it seems reasonable to assume that these words took the form of mimetic gestures or even sounds imitating whatever the shared object of attention was (likely food/carcasses or tools). As Studdert-Kennedy and Terrace (2017, p. 121) speculate, "[t]he vocal modality would have come to prevail, leaving hands and eyes free to go about their more important functions." Before processes such as grammaticalization took control of complex morphology, initial vocalizations would have been simple linearizations relying on pragmatic procedures to derive the full meaning of expressions (Murphy, 2016b). Yet Cataldo et al. (2018) conducted the first assessment comparing the efficiency of speech (unaided by gesture) with gesture and also gesture-plus-speech as tool-making transmission aids. They demonstrated that subjects instructed by speech alone underperformed in stone tool-making compared to subjects instructed through either gesture alone or gesture-plus-speech. They conclude that "gesture was likely to be selected over speech as a teaching aid in the earliest hominin tool-makers," and that "speech could not have replaced gesturing as a tool-making teaching aid in later hominins, possibly explaining the functional retention of gesturing in the full language of modern humans." They also suggest that speech may therefore have emerged for reasons unrelated to tool-making; it may have been a response to increased trade and more complex intra-group interactions bolstered by population increases.

In 1949, one of the most influential paleontologists of the twentieth century, Simpson (1949, 291–292), wrote:

> Man arose as a result of the operation of organic evolution and his being and activities are also materialistic, but the human species has properties unique to itself among all forms of life, superadded to the properties unique to life among all forms of matter and of action. Man's intellectual, social, and spiritual natures are altogether exceptional among animals in degree, but they arose by organic evolution.

It is common in the field for researchers to claim that because language is such a complex system – "altogether exceptional" (Corballis, 2017) – its evolutionary roots must extend very far back. As DeSalle and Tattersall (2017, p. 6) review, the first anatomical *Homo* exhibited "little if any of the zeal for change and innovation, and none of the ability to reconceptualise the world, that so richly characterize their modern language-endowed descendants." But these debates presuppose a clear understanding of what *language evolution* is, as distinct from the evolution of closely related capacities. When it comes to the relevance of the fossil record to questions of *speech evolution*, Wood and Bauernfeind (2011, p. 271) conclude their data review by claiming that "the fossil evidence for archaic hominins contains little, or no, reliable evidence about the speech capabilities of these taxa." But, going beyond fossils, what about the evolution of language and communication, distinct from speech? Assuming, as is commonly done, some form of relationship between symbolic communication and linguistic competence, there are a number of higher cognitive capacities that we share with our close relatives according to existing paleoanthropological accounts. Consider the Makapansgat manuport, a small stone (2 × 3 inches) found amongst Acheulean tools in South Africa in 1925 and putatively collected by *Australopithecus africanus* around 3 mya (other Acheulean tools are dated somewhat later). It seems to closely resemble a human face, suggesting that Australopithecus could grasp connections between arbitrary symbolic forms and abstract meanings; otherwise known as iconicity. Since this semantic property appears so deeply rooted in hominin evolution, this might explain its prevalence amongst early religionists (see also Peterson, 1999, 2018).

Examining the neural basis of primitive tool technology, Hecht et al. (2015) compared brain responses while learning either the basic Oldowan technique or the more complex Acheulean technique. The latter exhibited increased activation in the right inferior frontal gyrus and bilaterally in other regions, suggesting an increase in the requirement for cognitive control. Toolmaking typically involves the dominant hand making repetitive, rhythmic motions while the subordinate hand holds the object and occasionally rotates it (Uomini and Meyer, 2013). According to Uomini and Meyer (2013), hemispheric dominance arose due to the separation of competing neural processing strategies, one implicated in complex sequential behaviors like hand motions, and the other involved in coarse motor routines. Coordinating two different processes simultaneously (low-frequency and high-frequency motor commands) in what can arguably be described as a hierarchically organized form of behavior (though of limited hierarchy; Stout and Chaminade, 2012) may well have led to the selection for certain neural subroutines which the language system recruited when structuring the processing of units of different hierarchical complexity, i.e., when processing multiple syllables into a single word, and ultimately processing multiple words into a single phrase. Indeed, Morgan et al. (2015) discovered that students learned to make stone tools faster under verbal instruction, pointing to a potential co-evolution between toolmaking and speech (although it should be stressed that simply because verbal instruction enhances performance on a certain task, it does not follow that verbal abilities and this given task co-evolved). Note that this hypothesis does not lead to any causal explanation for language evolution (e.g., it does not commit one to the assumption that language evolved directly from toolmaking), it simply proposes that when the language faculty did emerge it was embedded within a sophisticated computational network.

Another related example comes from the Erfoud manuport, dated at around 300,000 years old and discovered in eastern Morocco. Seemingly collected by *H. erectus*, the manuport is a cuttlefish bone shaped like a phallus (Everett, 2017). What is the possible relationship of these findings to language evolution? Conceiving of language as a recursive combinatorial system involving the construction of hierarchically organized syntactic objects, generative linguists such as Hornstein (2009) or Chomsky (2010) would likely not be too impressed with a penis-shaped cuttlefish bone. Yet clearly the capacity to bind bodily concepts either to concrete instantiations or more abstract symbolic representations in the form of manuports involves some form of impressive semantic mapping of the kind subsequently exploited by the language system in anatomically modern humans. Moreover, the development of the 300–400,000-year-old Schöningen spears point toward a sophisticated culture amongst *Homo heidelbergensis*, since not only do they act as tools but they also have symbolic cultural meaning, such that the spear can denote the act of hunting in abstraction, i.e., in the absence of any particular hunt. And unlike many other tools used throughout the animal kingdom, Everett (2017, p. 143) notes that these spears display aspects of Peircean signs in that "only certain parts of the tools are meaningfully connected to their tasks, e.g., the edge of the tool." This greater degree of abstraction seemingly came about shortly before the time that language would have emerged among anatomically modern humans (300–200 kya), and so the generous and rapidly developing cognitive toolbox of *H. heidelbergensis* (a variant of *H. erectus*, or even identical according to some researchers) may well have been passed down to modern humans. *H. heidelbergensis* additionally had a great number of nerves linking the brain and tongue than its predecessors, suggesting that it possessed the ability to refine and control vocalizations.

With this toolbox at the ready, the bow and arrow was used by humans as early as 71 kya (McBrearty, 2012), a weapon which goes considerably beyond the complexity of the spear, likely involving a degree of sophisticated communication in order for it to be taught and implemented in a coordinated, strategic fashion. Likewise, most researchers concur that the capacity for complex symbolic thought (i.e., combining distinct symbolic representations in novel, "imaginative" ways, of the kind found in polysemy; Pustejovsky, 1995, 2008; Falkum and Vicente, 2015; Murphy, 2019b) was needed to construct bodily ornaments such as beads and decorative objects (Vanhaeren et al., 2006; Texier et al., 2010); both of which appeared around 100–60 kya.

The capacity for complex orthography, and potentially also the ability to associate symbolic meaning with indentations, can also be found as far back as 540 kya in the form of zigzag marks on a shell made by a member of *H. erectus* and found in Java. Interestingly, a sea voyage was likely made by the creator (from mainland Asia to Java), who might have represented the sea through these patterns. The intentional act of creating marks to represent abstract icons also provided an important pre-linguistic trait for anatomically modern humans, who presumably would have been able to externalize their new Language of Thought after the emergence of human-specific syntax in precisely the same way as *H. erectus*, with the exception of using such markings to represent more complex, composite representations, as opposed to simple concepts like SEA or FACE. Likewise, *H. erectus* crafted a wide number of tools (including choppers and pounders). These could not have feasibly been created systematically from any random motor sequence, but require planning and imagination, as well as the ability to communicate to others the methods of production. The expanded cognitive power required for mastering these procedures, which soon became a necessary part of survival (in particular in the event of tribal warfare), may well have led to an important role for natural selection: namely, selection for expanded fronto-parietal circuits to satisfy the growing demand for cognitive control networks. Thus, we find the world's oldest piece of art, the 250 kya Venus of Berekhat Ram, a rock carved in a female shape with evidence of intentional red ochre coloring for decoration, an object crafted with precision and imagination.

These ideas – of syntax ultimately being couched within pre-existing semantic properties – are quite distinct from the hypothesis proposed by Everett (2017). His claim is that "with symbols + concatenation, there is language" (2017, p. 160). While a certain amount of compositionality might be derived from a semantic system relying on this architecture, hierarchically organized phrases plus long-distance dependencies cannot emerge from this. Combining representations of any format into syntactically hierarchical phrases is not a job for symbolism and concatenation alone (Murphy, 2015, 2016a). Likewise, the engraved ochre and bones found in Blombos Cave are suggestive of symbolic manipulations, yet as Botha (2011, p. 307) notes any links to syntactic language are highly questionable since "beads, ochres, and engraved bones cannot stand as evidence for modern cognition, including language, unless it is specified what cognitive abilities these artifacts require." Indeed, although the use of pigments pre-dates Blombos Cave and even implicates Neanderthals, these were non-symbolic and displayed little variation (Neanderthal pigments were generally black, for instance).

Finally, one of the core characteristics of the tools of early *H. sapiens* is that they were crafted for durability just as much as immediate usefulness. This suggests a familiarity not only with symbolic behavior, but with long-range planning. These planning and strategizing capabilities are neurologically and computationally separate from purely linguistic processes, suggesting that modern cognition demanded certain developments in executive reasoning skills as well as the evolution of language.

The general picture that emerges here is the following: The Oldowan tools dated around 3 mya are suggestive of dexterity, motor control and intentional modifications of inanimate objects; the Acheulean tools dated slightly later (perhaps around 2 mya) are suggested of hierarchical cognition and/or complex motor planning, along with complex emotions. The axes, cleaver and spears of *H. heidelbergensis* dated around 400 kya are suggestive of visual imagination, emotional control, symbolism, and possibly a sense of self. The Levallois method is generally dated around 300 kya, and is suggestive of advanced hierarchical cognition, tuition, and an unusual degree of patience. Lastly, the technology of modern *H. sapiens* dated around 200 kya is suggestive of an improved memory, creativity, and an awareness of past and future.

DOMESTICATION

Closely tied to the theme of language evolution is the broader, and related (indeed, arguably identical) theme of *human evolution*. If we define *H. sapiens* based on derived skeletal features, then the fossil record would place human origins somewhere in the

African late middle Pleistocene. The relevant fossil data includes Omo Kibish 1 and the Levantine material from Skhul and Qafzeh. Some of the oldest morphologically modern humans have been found at the Omo Kibish sites, and date to ∼195 kya (McDougall et al., 2005). Yet the genetic data indicates that both anatomically modern humans and *Homo neanderthalensis* shared a common ancestor in the middle Pleistocene (400–700 kya), a date some 200 kya earlier than the fossil-determined date.

Stringer (2016) notes that findings of this kind suggest that the morphology of *sapiens* exhibited no linear progression, and "there was chronological overlap between different 'archaic' and 'modern' morphs" (2016, p. 1). Extant humans exhibit a number of shared traits, including a high neurocranium, a small face retracted under the frontal bone, small discontinuous supraorbital tori, and a narrow trunk and pelvis (Stringer, 2016). Anatomically speaking, it is possible to detect humans in the fossil record through focusing on these and broader features like cranial globularity and basicranial flexion (Arsuaga et al., 2015). Particularly relevant for language is a certain feature of the cranial vault: The parietal region is highly distinctive in humans, being expanded in certain areas (Bruner, 2010). Modulating and strengthening the connections of this expanded parietal region with other regions, such as anterior temporal regions and subcortical structures like the thalamus, may have contributed to novel cross-modular communication.

In this connection, it is increasingly becoming clear that the topic of *domestication* has clear potential to inform our understanding of human brain evolution. The notion that anatomically modern humans are a fundamentally domesticated species has a long and rich history, dating back to Darwin (1871) and Boas (1938), with the latter commenting that "[m]an is not a wild form, but must be compared to the domesticated animals. He is a self-domesticated being" (Boas, 1938, p. 76). Concerning the general processes of self-domestication, Boas added that "[i]t is likely that changes of mental character go hand in hand with them" (1938, p. 140), and it is only very recently that researchers have been able to propose concrete hypotheses which expand on these speculations.

Domesticated species (including dogs, cats, foxes, pigs, and sheep) are usually defined based on their shared phenotypic traits, referred to collectively as the "domestication syndrome" (Zeder, 2012) and which include depigmentation, reduced ears, shorter muzzles, smaller teeth, smaller cranial capacities, and a reduction of sexual dimorphism (feminisation). Many of these features are exhibited by anatomically modern humans, and in fact distinguish humans from Neanderthals (Theofanopoulou et al., 2017), and they may also reflect a generalized deficit in the neural crest, an embryonic structure responsible for pigmentation and the cranial skeleton, amongst other things (Wilkins et al., 2014). Domesticated animals used to be regarded as entirely separate species but are now thought of as sub-species of their wild progenitors. Le Douarin (1980) discovered that transplanting neural crest cells from chicks to quails resulted in the chimeric hatchlings producing intermediate chick/quail vocalizations, suggesting that the process of self-domestication, involving the neural crest, contributed in some fashion to the emergence of vocal learning. Interestingly, Theofanopoulou et al. (2017, p. 4) document how interspecific domestication events suggest that "the selective pressure for our self-domestication need not have been qualitatively different from those experienced by other species." For instance, the silver fox (*Vulpes vulples*) was intentionally domesticated through a project initiated by Belyaev (1979) based on a single criterion: tameness toward humans. After only 20 years of selection for tameness, a range of features typically associated with domestication emerged, suggesting a strong, causal link between the above noted phenotypic characteristics of domesticants.

It is therefore likely that selection for tameness, prosocial behavior or related traits associated with the syndrome brought about human self-domestication after the split from our last common ancestor. Self-domestication can potentially explain – "for free" – a number of human-specific traits, with the possible exception of the descended larynx, an explanation for which remains in relative obscurity. Speaking to this hypothesis, recent work suggests that humans, unlike monkeys, are adept at turning competitive situations into cooperative ones (Marquez, 2017). Tomasello et al. (2005, p. 685), discussing "shared intentionality," note that "it is almost unimaginable that two chimpanzees might spontaneously do something as simple as carry something together or help each other make a tool." More generally, as Theofanopoulou et al. (2017, p. 12) note: "It is also not unreasonable to suspect that byproducts of the domestication process, such as enhanced sensory-motor perceptual and learning pathways, may provide a foundation for more complex communicative abilities, including vocal learning abilities."

Recent work has emphasized the potential for studies of dog vocal social perception to enhance our understanding of how linguistic and non-linguistic signals are represented in the mammalian brain in particular given that dogs have lived in anthropogenic environments from at least 32–16 kya (Andics and Miklósi, 2018). This perspective goes somewhat beyond the standard focus on great apes, giving the study of vocal social perception a broader mammalian basis. It has been argued in the literature that dog domestication enabled this species to survive in small human groups (Serpell, 1995), fast becoming man's "best friend," with this process selecting for dogs with the genetic potential to develop human-compatible behaviors. Dog brains also appear to have dedicated voice areas, preferring conspecific vocalizations over other sounds (Andics et al., 2014). These areas are located in anterior temporal regions, including the bilateral temporal poles. One possible interpretation of these findings, as Andics and Miklósi (2018, p. 60) note, is that "conspecific preference in dogs and humans relies on homologous brain structures, implying that voice areas have been there in the last common ancestor of the two species, but convergent evolution provides an alternative interpretation that voice areas developed independently in the ancestors of dogs and humans, after their lineages split."

The importance of examining the brain in order to properly distinguish humans from Neanderthals is highlighted in recent work in paleoneurology. Mounier et al. (2016) document how endocranial features are more informative than features of the calvarium (supporting research efforts geared toward domestication) and how human endocranial anatomy dramatically changed during the end of the Middle Pleistocene. Cultural development seems to have appeared alongside domesticated features like a smaller braincase, with a reorganization of the cranium altering many neural features.

Wrangham (2009) maintains that the cultural developments of anatomically modern humans are the result of self-domestication via inhibiting aggression and related traits. His line of research points to comparable developments within certain ape societies. For example, while chimpanzees display a range of cooperative traits their culture is typically plagued by aggression and violence (Hare et al., 2012). Bonobos (pygmy chimpanzees), in contrast, display a juvenile appearance (in line with domestication models) and live in far more peaceful societies (though, it should be noted, not as peaceful as stereotypes would suggest due to clear carnivorous tendencies). Like humans, bonobo societies are much larger than those of chimpanzees, with the rapidly increasing size of early human tribes likely playing a role in their domestication. As Aboitiz (2017, p. 452) summarizes: "As we domesticated other species, we adapted ourselves to the process of domestication, forming an evolutionary circle that maintained our genetic evolution and drags other species with it." This cyclic process of self-domestication involved adapting to the needs of human groups while also domesticating a range of plants and animals in ways dynamically responding to such needs, with the newly domesticated plants and animals in turn influencing the social structure of human societies (see also Murphy, 2019a).

Turning to a related field of study, Okanoya (2012, 2013) reports that comparisons of the songs of wild finches (white-rumped munia) and domesticated finches (Bengalese finch) suggest that the latter produced songs of greater complexity, differing in acoustical morphology and the order of elements. Lansverk et al. (2018) replicate and expand on these results and also explore their genetic underpinnings. The sound density was also found to be 14 dB higher in Bengalese finches than in white-rumped munias during recordings from identical settings. The most recent research in this direction has even suggested that domesticated birds have smaller brains but a larger cortex, in particular the forebrain (Olkowicz et al., 2016). As such, domestication seems broadly responsible for increases in syntactic complexity, with the complex syntax of Bengalese finch songs developing from simple neurological changes (Katahira et al., 2013).

In summary, it appears from recent evidence that self-domestication helped lay the groundwork for enhancing in modern humans some of the communicative, semantic and syntactic capacities of our ape ancestors.

THE CEREBELLUM AND SPEECH

Although left-frontal and parietal regions enjoy the most attention in discussions of language evolution, I would like to briefly address the potential importance of the *cerebellum*, which is increasingly being implicated in language processing. Of course, there are many other regions in the brain for which the same type of evidence presented below could be used in support of the idea that they are important for language, but the cerebellum more tightly fits into the present theme of brain shape modification.

The human cerebral cortex is approximately 3 millimeters in depth, while the cerebellum is considerably larger and contains 60 out of the brain's 86 billion neurons. Yet its role in higher cognition remains somewhat unclear. Pursuing the above line of inquiry, Ogihara et al. (2018) conducted a three-dimensional geometric morphometric analysis of reconstructed Neanderthal and early human endocasts. Their results indicated that ecto- and endocranial shapes are quantitatively different between the two species. The cranium of early humans displayed relative enlargement of the cerebellar region and a notable parietal expansion. This is perhaps the strongest evidence that the neuroanatomical organization of the two species was significantly distinct. Following directly on from this documented cerebellum expansion, Tanabe et al. (2018) note that while the cerebellum has typically been seen as being involved largely in fine motor control, an emerging consensus is that this region is also involved in certain cognitive functions, including language. It exhibits a unique gross anatomy and microstructure, and the cerebellar cortex contains circuitry functioning as a learning system able to construct and store internal models of the world. Tanabe et al. (2018) show that the greater volume of the cerebellar cortex, the greater number of internal models it is able to construct and store. It seems likely that the cerebellum is therefore implicated in forms of long-term memory, with some of the complex representations it stores being constructed initially by the language system. In this sense, it may act as a post-linguistic long-term storage site, functionally distinct from parts of Broca's area (e.g., BA 44 v, following standard sub-parcellation) which seem to act as a short-term memory "buffer" site for phrase structures. Finally, cerebellar dysfunctions in humans lead to distinct speech motor deficits referred to as ataxic dysarthria (Ackermann, 2008; see also Murphy and Benítez-Burraco, 2017). The cerebellum is assumed to be involved in the control of coarticulation effects given its involvement in sequencing syllables into fast, rhythmically structured larger utterances. Nozaradan et al. (2017) also provide EEG evidence that the cerebellum and basal ganglia are involved in the neural representations of rhythmic sequences, in particular those demanding the encoding of precise sub-second events (see also Obleser et al., 2017).

More recently, Smaers et al. (2018) investigated the lateral cerebellum (a structure unique to mammals) across a range of species and mapped its evolutionary diversification, finding that relative volumetric changes of the lateral cerebellar hemispheres are correlated with measures of domain-general cognition in primates. These are furthermore characterized by a combination of parallel and convergent shifts toward similar levels of expansion in distantly related mammalian lineages. This suggests that increased behavioral complexity (for our purposes, of the kind found in the emergence of language) from a range of directions may be traced back to a common selection on a shared neural system, the cerebellum. This implies that this brain region aided certain other forms of higher cognition in a range of mammals, while in humans it seems to have aided rhythmicity and memory load, directly exploited by the language system.

Deepening these connections, Pidoux et al. (2018) show that the cerebellum provides a strong input to the song-related basal ganglia nucleus in zebra finches. Cerebellar signals are transmitted to the basal ganglia via a disynaptic connection through the thalamus, before being conveyed to their cortical target and to the premotor nucleus controlling song production. These authors also showed that cerebellar lesions impair juvenile song learning.

As such, paleoneurological evidence bearing on the morphology of the cerebellum will likely inform our understanding of when certain language-related capacities emerged.

FUTURE DIRECTIONS

The unanswered questions emerging from this discussion cut across a range of domains: Which features of (self-)domestication have had an impact on the language system architecture? How does the speed of the molecular clock impact either saltationist or adaptationist hypotheses concerning the emergence of language? What are the potential ways domestication can influence the externalization component of a given species? Which factors (e.g., nutrition, climate) had the potential to impact features of human cognition relevant to language comprehension during the course of modern human evolution? To what extent could future studies of archaic hominin admixture provide insights into the evolution of language? What specific brain regions were impacted by globularisation, and how did this process impact language (and language-related) processes? How might globularisation have impacted higher cognition in other species?

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The author confirms being the sole contributor of this work and has approved it for publication.

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Hypotheses for the Evolution of Reduced Reactive Aggression in the Context of Human Self-Domestication

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Parallels in anatomy between humans and domesticated mammals suggest that for the last 300,000 years, *Homo sapiens* has experienced more intense selection against the propensity for reactive aggression than other species of *Homo*. Selection against reactive aggression, a process that can also be called self-domestication, would help explain various physiological, behavioral, and cognitive features of humans, including the unique system of egalitarian male hierarchy in mobile hunter-gatherers. Here I review nine leading proposals for the occurrence of self-domestication in *H. sapiens*. To account for the domestication syndrome, proposals must explain what led to a decline in fitness of highly aggressive males, and why the explanatory factor applies only to *H. sapiens* and not to other species of *Homo*. The proposed explanations invoke genetic group selection; group-structured culture selection (also known as cultural group selection); social selection by female mate choice; social selection by male partner choice; increased self-control; cooperative breeding; high population density; use of lethal weapons; and language-based conspiracy. Most of these proposals face difficulties in accounting for the origins and/or maintenance of reduced reactive aggression. I conclude that the evolution of language-based conspiracy, which is a form of collective intentionality, was the key factor initiating and maintaining self-domestication in *H. sapiens*, because it is the most convincing mechanism for explaining the selective pressure against individually powerful fighters. Sophisticated language enabled males of low fighting prowess to cooperatively plan the execution of physically aggressive and domineering alpha males. This system is known today as a leveling mechanism in small-scale societies. Group-structured culture selection possibly accelerated the process.

Keywords: self-domestication, *Homo sapiens*, reactive aggression, social selection, collective intentionality, alpha-male, leveling mechanism, execution

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INTRODUCTION

Darwin (1868) showed that domesticated mammals tend to share a variety of similarities in their appearance, anatomy and behavior, a phenotypic suite now called the domestication syndrome. Working with silver foxes *Vulpes vulpes* and mink *Mustela vison*, Belyaev (1969) showed that features of the domestication syndrome were produced by selection purely for docility, i.e., for a low propensity for reactive aggression (Trut, 1999). Selection for tameness in chickens *Gallus gallus domesticus* also produces several reproductive and physiological changes similar to those found in the mammalian domestication syndrome (Agnvall et al., 2017). The presence of a domestication syndrome therefore appears to be a signal of selection again reactive aggression.

It is interesting, therefore, that evidence has recently been increasing for humans *Homo sapiens* having a domestication syndrome (Leach, 2003; Francis, 2015; Henrich, 2016; Hare, 2017; Hare and Wrangham, 2017; Theofanopoulou et al., 2017; Wilkins, 2017; Benítez-Burraco et al., 2018; Sánchez-Villagra and van Schaik, 2019; Wrangham, 2019). While there are various physiological, behavioral, cognitive, and genetic similarities between *H. sapiens* and domesticated animals, the anatomical evidence is particularly strong (Leach, 2003). Leach (2003) considered four features used by archeologists to recognize a domesticated species in the fossil record, namely a reduction in body mass, shortening of the face accompanied by a reduction in tooth size, reduced sexual dimorphism due to feminization, and a reduction in cranial capacity. Leach showed that all four traits are found in *H. sapiens*, although cranial capacity was not reduced until the end of the Pleistocene and the significance of its reduction has been challenged (Ruff et al., 1997). Facial width and brow-ridge projection have also declined in *H. sapiens* (Cieri et al., 2014). Currently the earliest record of a lineage of *H. sapiens* comes from around 315,000 years ago from Jebel Irhoud, Morocco (Hublin et al., 2017). The Jebel Irhoud specimens have short faces, small teeth, and reduced brow-ridges compared to pre-*sapiens* ancestors, making them the earliest human specimens to show features of the domestication syndrome. These points suggest that Pleistocene *Homo* experienced selection for self-domestication starting before 300,000 years ago.

The evidence for a domestication syndrome in *H. sapiens* suggests that our species evolved greater docility than pre-*sapiens* ancestors (Hare, 2017; Wrangham, 2019). Behavioral comparisons with prehistoric species are speculative. In support of humans' relative docility, however, *H. sapiens* has frequencies of within-group aggressive conflict that are two to three orders of magnitude lower than those found among wild chimpanzees *Pan troglodytes* and bonobos *P. paniscus* (Wrangham, 2019). In support of the behavioral significance of recent anatomical changes, living adult males with relatively narrower faces tend both to be less reactively aggressive and to be perceived as being less aggressive (Carré and McCormick, 2008; Haselhuhn et al., 2015), to the point of being assessed as having more human-like minds (Deska et al., 2018). Anatomical and behavioral data are thus consistent with humans having undergone a process of selection for reduced aggression during the last 300,000 years.

The selection pressures that favored reduced aggression in *H. sapiens* are a matter of debate, and are the topic of this paper. Human aggressiveness has recently been argued to come in two major forms, reactive (or impulsive) and proactive (or premeditated), each with their own distinctive neurobiology (Wrangham, 2018). The high degree of docility that is characteristic of humans and domesticated animals depends on a low propensity for reactive aggression, but what relationship it has with proactive aggression, if any, is unknown (Wrangham, 2018). In this article I consider the decline of aggressiveness only with respect to reactive aggression.

I consider two kinds of explanation for the assumed decline of reactive aggression, direct and indirect. Direct explanations attempt to understand how aggressiveness itself became reduced. Indirect explanations, by contrast, have been designed to explain why cooperation has been favored, rather than aggressiveness being reduced. I include indirect explanations, even though their proponents did not necessarily apply them to the problem of reduced aggressiveness, because a high degree of cooperation tends to be facilitated by reduced aggression (Simon, 1990; Melis et al., 2006; Cieri et al., 2014). Hypotheses for the evolution of increased cooperation could therefore in theory contribute to explaining why docility evolved (e.g., Henrich, 2016; Richerson et al., 2016).

Nine proposals are considered below, selected as being the most prominent explanations for either reduced aggressiveness or increased cooperation in the human lineage (**Table 1**). They

TABLE 1 | Evolutionary scenarios for selection against reactive aggression (i.e., self-domestication) in human evolution, applied to *Homo sapiens*.

Scenario	Merits	Problems
1. Genetic group selection	Theoretically plausible if groups sufficiently stable	Behavioral similarities between humans and chimpanzees not explained
2. Group-structured culture selection (GSCS)	Likely influenced much *H. sapiens* behavior	Unlikely to have been important 300,000 years ago. Selection against aggression not explained
3. Social selection by female mate choice	Female choice currently important	Constraints on violent males not explained
4. Social selection by choice of cooperative task partners	Male teamwork likely important	Constraints on violent males not explained
5. Self-control	Stronger self-control in species with bigger brains	Constraints on violent males not explained
6. Cooperative breeding	Extensive cooperation in human reproduction, associated with low aggression	Cooperating breeding proposed to characterize other *Homo* species, not just *H. sapiens*. Selection against aggression not explained
7. Population density	High population density sometimes associated with reduced aggression	*H. sapiens* population density apparently low in much of the past. Selection against aggression not explained
8. Use of lethal weapons	Facilitated control of reactive aggressors by safe killing	Likely too early to apply specifically to *H. sapiens*
9. Language-based conspiracy	Facilitated control of reactive aggressors by safe killing	Timing of language skills is speculative; hard to test (relevant cultural practices extinct)

Merits and problems shown are not exhaustive. See text for citations and further discussion.

attribute selection for increased docility and/or cooperation to: genetic group selection; group-structured culture selection (also known as cultural group selection); social selection by female mate choice; increased self-control; social selection by male partner choice; cooperative breeding; high population density; use of lethal weapons; and language-based conspiracy. The first five of these candidate explanations are indirect, meaning that they have been used more to explain the evolution of humans' unusual extent of cooperation rather than accounting for reduced reactive aggression *per se*. The proposals are potentially complementary.

Because I consider so many explanations I do not review any of them in detail. Instead, my aim is to present them in a fresh light, given two relatively new ideas (Wrangham, 2019). The first new idea is that self-domestication is produced by selection against reactive aggression; the second is that self-domestication began shortly before 300,000 years ago, and was responsible for the origin and evolution of many of *H. sapiens*' unique traits. In short, the core problem animating this enquiry is why, throughout its evolution, *H. sapiens* experienced consistent selection against reactive aggression.

RESULTS

Context for Selection Against Reactive Aggression

Based on the signals of human domestication found throughout the last 300,000 years, the species in which selection first occurred against male reactive aggression would have been the mid-Pleistocene *Homo* that give rise to *H. sapiens*. I follow the assumption (e.g., Gintis et al., 2015) that this ancestral *Homo* species, sometimes called *Homo heidelbergensis*, would have lived in social communities and would have had dominance hierarchies typical of primates living in multi-female, multi-male groups. Specifically there would have been an alpha male who achieved his position by physically defeating lower-ranking males in one-on-one combat. The alpha would also have dominated all females, and would have predictably experienced higher fitness than other males. This system is found in chimpanzees (Wroblewski et al., 2009), gorillas (*Gorilla* spp.) (Nsubuga et al., 2008; Breuer et al., 2012), savanna baboons (*Papio* spp.) (Alberts et al., 2006; Baniel et al., 2017), and most other primates living in multi-female, multi-male groups.

In a few such species this system is not found. In bonobos, there is an alpha male, but he ordinarily owes his position to the support of his mother rather than to his ability to fight alone, and he is not necessarily dominant to the alpha female (Surbeck et al., 2011). This exception to the general rule of alphas achieving their top rank through personal fighting ability is understandable, since bonobos show evidence of having been self-domesticated (Hare et al., 2012; Wrangham, 2019). In other words selection has acted to reduce the propensity for reactive aggression in bonobos, compared to a chimpanzee-like ancestor, such that male bonobos who use reactive aggression to achieve an alpha position by being the most effective fighter would not tend to achieve maximal fitness.

Humans are also exceptions to the typical type of primate dominance hierarchy, because among humans alpha males do not achieve their position by defeating all other group males in one-on-one fights. Instead, male dominance hierarchies fall into two main types. In some societies a coalition of the majority is able to prevent any individuals from dominating access to preferred resources (Boehm, 1999). In these cases, called a "reverse dominancy hierarchy" or "counter-hierarchy" there are no alpha males (Boehm, 1993). Reverse dominance hierarchies are found in mobile hunter-gatherers and some small-scale horticulturalists. They can be contrasted with bonobo hierarchies, which have alpha-males (Surbeck et al., 2011, 2019).

In the other main system, an individual political leader is recognized. The leader achieves his or her position in a variety of ways, such as by following societal rules, via a novel consensus, or by violence. The critical difference from the typical primate system is that, whatever the mechanism by which a man or woman becomes leader, it involves coalitional power rather than individual fighting prowess (Gintis et al., 2015; Wrangham, 2019).

Given these assumptions of a primate-like dominance system in mid-Pleistocene *Homo*, any explanation of the evolution of a reduced propensity for male reactive aggression faces two important challenges.

First, it must account for the failure of the most individually effective fighters to dominate access to resources and thereby maximize their fitness. The simplest hypothesis is based on the assumption that the present informs the past. Among present-day bonobos, for example, males who are aggressive to females are suppressed by coalitions of females. As a result, a plausible partial explanation for the evolution of reduced reactive aggression in bonobos is that ecological changes allowed female proto-bonobos to co-exist more readily than before, which enabled them to use coalitions more effectively against domineering males (Hare et al., 2012).

Similarly, the societies of contemporary mobile hunter-gatherers offer a guide to reconstructing late Pleistocene societies. Among hunter-gatherers there is no consistent evidence of females using coalitions to control excessively aggressive males. Instead, the excesses of would-be despots are suppressed by coalitions of adult males, who resort to execution when lesser mechanisms fail (Boehm, 1999, 2012). If this mechanism applied throughout the existence of *H. sapiens*, it would explain how there was selection against the best individual fighters [see (8) and (9) below].

The second challenge is that the explanation for selection against reactive aggression must apply only to *H. sapiens*, since it is the only species of *Homo* known to exhibit a domestication syndrome.

Proposed Explanations

(1) Genetic Group Selection

In its traditional formulation, genetic group selection (hereafter: group selection) is the evolution of traits based on the differential survival and gene production of groups (Eldakar and Wilson, 2011). Group selection has been proposed as a mechanism for promoting parochial altruism, meaning altruism restricted to "one's own ethnic, racial, or other group" (Choi and Bowles, 2007: 636). The core idea is that the value to group members of cooperating with each other (in conflict against neighboring groups) would be so high that it would overcome the value of being selfish toward each other, and lead to selection against selfishness. Marean (2015) developed a version of this hypothesis that suggested why selection in favor of cooperation was more intense in the origin of *H. sapiens* than in other *Homo*. He pointed to increasing exploitation of dense and predictable food resources, leading to higher population density, and more aggressive defense of territories. Such ideas suggest that the evolution of prosociality could include selection against a high propensity for reactive aggression.

Even if intergroup conflict became more important in *H. sapiens* than in earlier *Homo*, however, the parochial altruism hypothesis is challenged by behavioral similarities between humans and chimpanzees. Starting with Darwin (1871), group selection theories for human cooperation have assumed that humans have a uniquely high intensity of intergroup conflict. However chimpanzees have been found to have rates of death from intergroup aggression in the same order of magnitude as mobile hunter-gatherers (Wrangham et al., 2006). Group selection theory also requires a high degree of genetic differentiation among groups. Yet estimates of the degree of between-group genetic differentiation in hunter-gatherers and other small-scale human societies likewise prove to be similar to those among chimpanzees, if not slightly higher among chimpanzees (Langergraber et al., 2011). The group selection argument thus does not differentiate between humans and chimpanzees, even though only humans, and not chimpanzees, have experienced selection against reactive aggression.

More generally, group selection is inherently unlikely to have had major effects in humans given the low extinction rates and high permeability of human groups. Whether hunter-gatherer societies are considered at the level of the local group (or band, averaging 25–50 individuals) or the ethnolinguistic society (averaging nearer 1000), the lifespan of a typical group allows innumerable immigration events. Those facts are incompatible with the idea that selection pressures against individually selfish behavior would be significant (West et al., 2007).

Finally, there is reason to question the core assumption that success in intergroup conflict is increased by a reduction in within-group conflict. This problem is discussed below (2)

(2) Group-Structured Culture Selection (GSCS)

Group-structured culture selection (GSCS), also known as cultural group selection, is concerned with the selective spread or reduction of cultural behaviors that operate at the level of a social group (Zefferman and Mathew, 2015; Richerson et al., 2016). Examples of such behaviors are legal institutions or styles of warfare. GSCS theory is often applied to cultural behaviors that have changed recently, e.g., the last few hundred years. In those cases it has little relevance for genetic evolution of populations, and none for genetic evolution of the species as a whole. However, changes in individual cultural behavior that occurred on a longer time-scale are known to have led to gene-culture coevolution, e.g., the development of cooking, or milk-drinking by adults (Wrangham, 2009; Curry, 2013; Henrich, 2016). This suggests that similar effects could have occurred for changes in group cultural behavior also. While such selection is theoretically possible, to my knowledge no cases have yet been documented of GSCS leading to genetic change. Nevertheless, if group cultures in the form of social norms occurred as early as 300,000 years ago, GSCS might have contributed to selection against reactive aggression.

Such an early time is challenging for theory. In the words of Richerson et al. (2016, p. 6): "If genes for docility were selected early in the hominin lineage before we have evidence for sophisticated culture, they are less likely to have been a product of culture-led gene-culture coevolution than if they evolved in the last 150,000 years as culture increased to modern levels of sophistication." The culture of ∼300,000 years ago included the first known use of ocher, the first known Levallois tools, and far more extensive transport of stone tools than before (Brooks et al., 2018). Whether or not these advances reflect a sufficiently sophisticated level of cognition that GSCS could have influenced norm psychology does not appear to have been discussed.

If group-structured culture selection is indeed argued to have fostered reduced reactive aggression in the origin of *H. sapiens,* the question would be how. A prominent candidate mechanism (normally discussed without a specific date in mind) is the "tribal social instincts hypothesis" (Richerson and Boyd, 1998). This hypothesis suggests that groups in which there were norms of parochial altruism would have been especially successful in intergroup competition. As a result, the norm for parochial altruism would spread by GSCS. Gene-culture coevolution would then include selection in favor of an increasingly parochial-altruistic psychology: tendencies for docility and conformity would be favored because individuals with those characteristics would readily acquire group norms (Richerson et al., 2016). Applying the hypothesis specifically to the problem of self-domestication, selected effects could in theory include reduced tendencies for reactive aggression, on the traditional premise that groups in which males competed more aggressively with group members would be less effective at intergroup conflict (e.g., Zhang et al., 2019).

While the tribal social instincts hypothesis is thus theoretically attractive, it faces the difficulty that successful intergroup conflict is not necessarily associated with reduced within-group aggression. In chimpanzees, classically violent alpha-male behavior within communities is associated with the most intense and lethal intergroup conflict known in non-human primates (Muller, 2002; Wilson et al., 2014). Likewise cross-cultural studies in humans consistently find that higher frequencies of war are correlated with higher, not lower, frequencies of interpersonal aggression (Ember and Ember, 1994). In a related test, across 15 species of monkeys no relationship was found between intergroup conflict and prosocial behavior (grooming) among males, although a positive relationship was found among females (Majolo et al., 2016). Such findings mean that a specific theory is needed to explain why intergroup conflict would have led to reactive aggression being selected against more intensely in *Homo,*∼300,000 years ago, than happens in other primates.

An alternative proposal that could have involved GSCS attributes selection against reactive aggression to the emergence of language-based conspiracy that would allow execution of aggressive individuals. I consider this proposal below (9)

(3) Social Selection by Female Mate Choice

Social selection occurs when "choices made by other individuals influence fitness and change gene frequencies" (Nesse, 2009). Female choice of mates and male choice of task partners have been specifically proposed as forms of social selection that could have promoted cooperative behavior (and by inference, reduced aggressive behavior). I consider the two types separately.

Female choice of less aggressive males as mates was proposed by Cieri et al. (2014) and Gleeson and Kushnick (2018) as a mechanism that could promote self-domestication, because females who choose less aggressive males can benefit by their mates' greater investment in shared parenting effort. Gleeson and Kushnick (2018) tested this idea among humans by assessing whether the degree of sexual dimorphism in height was reduced in societies where women have higher social status. In support, they found that in societies with higher-status women (who were presumed to have more freedom to choose their mates), men were relatively short (suggesting reduced selection for male aggressiveness).

There is an important difficulty for the female mate choice hypothesis, however: it does not account for the reproductive failure of intransigently despotic males. Before males had evolved their reduced aggressiveness, female choice would have been a weak force in the face of the physical dominance and coercive behavior of bullying males. Comparative data on primates with high levels of male aggression illustrate the problem. Among chimpanzees and chacma baboons *Papio ursinus*, detailed studies show that aggressive males are routinely able to coerce conceptible females into mating, even when those females resist them as mates (Muller et al., 2011; Baniel et al., 2017). Admittedly female choice of lower-ranked males can be so effective in primates that the alpha male's mating success is lower than expected (Nsubuga et al., 2008; Feldblum et al., 2014). Nevertheless, alpha-males still tend to obtain the largest share of paternity (Dubuc et al., 2014). Among living human populations males are already self-domesticated, which means that the power of female mate choice has been enormously elevated compared to 300,000 years ago. Similarly, in bonobos female choice is apparently very powerful: compared to chimpanzees, high-ranking male bonobos are relatively strongly preferred as mating partners by females, and they achieve a higher proportion of paternity (Surbeck et al., 2019).

How females of a mid-Pleistocene *Homo* could have acquired sufficient power to resist an aggressive male who intended to coerce her, against her will, is therefore a problem for the female mate choice hypothesis. Assuming that she would not have had the physical ability to freely express her choice, she would have had to rely on coalitionary help. This means that female choice alone would not have led to self-domestication. I discuss the use of coalitions below (8) and (9).

It should also be noted that nowadays, despite much craniofacial feminization and presumed behavioral feminization of males for some 300,000 years, human males are still capable of extensive coercion of females (Muller and Wrangham, 2009).

A further unanswered problem is why mate choice would have been different in the immediate ancestors of *H. sapiens* from other Pleistocene *Homo*.

In sum, mate choice by females probably became increasingly important during the later Pleistocene, and especially during the Holocene, as a result of males becoming less reactively aggressive. Female choice alone, however, appears incapable of explaining how, before males became the less aggressive form found today, self-domestication began.

(4) Social Selection by Choice of Cooperative Task Partners

On the assumption that humans benefit by cooperating in gathering, hunting, warfare and other tasks, social selection has likely been important in promoting altruistic, and non-competitive behavior within groups (Nesse, 2009). This general idea has been elaborated particularly clearly by Tomasello (2016), who presented an explanation for the evolution of morality that included a proposal for the reduction of aggressiveness in *H. sapiens*. Tomasello called it the "interdependence hypothesis."

According to the interdependence hypothesis the initial influence on the road to a human style of morality occurred around 400,000 years ago when there was a "disappearance of individually obtainable foods" (Tomasello, 2016: 136). Tomasello (2016) then cited three processes that could have been responsible for shifting early humans away from a primate-style reliance on social dominance to settle disputes.

First, due to this ecological change, mid-Pleistocene *Homo* were forced to collaborate in the food quest, rather than foraging individually as they had until then. The result was a new kind of interdependence, such that individuals who were collaborative and less selfish were favored: cooperators fed better, for instance, than those who were not chosen as foraging partners. Cooperative defense against predators was also important when scavenging meat from carcasses. Effective cooperation depended on a reduction in selfishness and aggressiveness, and on a concomitant increase in sympathy and shared intentionality.

Second, pair-bonding was initiated. As a result males recognized their offspring and spent time with them. Selection favored a low propensity for male aggression because offspring were thereby better protected from the father's potential violence.

Third, childcare became more cooperative. This influence is considered below (6).

According to Tomasello (2016: 43) "It was thus this pair-bonded, child-caring, relatively tolerant and gentle creature – a self-domesticated great ape – who entered into the new and still more collaborative lifeways that we will be positing as the evolutionary origins of uniquely human cooperation and morality."

Tomasello's proposal has the merit of suggesting a specific ecological change that could have solved, through various identified pathways, the core problem of how a reduced propensity for aggression was favored. Admittedly his specific claims are debatable. For example there is no direct evidence as to whether, around the time that *H. sapiens* evolved, foods could no longer be collected individually, teamwork against predators became much more important, or pair-bonding began. Thus the notion of a relevant ecological change is entirely speculative. Regardless of those issues, I believe there is a more damaging problem.

Similar to the problem with the female mate choice hypothesis, the difficulty is that Tomasello does not discuss what would stop a determined, physically powerful male from exerting his fighting ability at the expense of others in his group. Suppose that teamwork indeed became more important in the food quest, that a despotic male would have been excluded as a partner, and that as a result, the despotic male would have become a less effective forager than his cooperating peers. Tomasello's implied conclusion is that the despot would feed poorly, and that as a result his style of behavior would have been selected against. By analogy with non-human primates such as chimpanzees or savannah baboons, however, an alternative conclusion must be considered. The despotic male would improve his lot by seizing the choicest foods that others produced: his physical dominance would allow it. Like a male lion *Panthera leo* feeding off the kills brought down by females, the determinedly aggressive and effective fighter would continue to have high fitness thanks to his ability to commandeer food, mates or other resources from others in the group. His ability to use force to impregnate more females than his expected share would mean that any injury he might cause to his offspring would be easily compensated. But anyway, injuries to offspring would have been unlikely from even the most aggressive males, to judge from the tolerant relationships of males with their offspring among species such as chimpanzees, gorillas, baboons or lions.

In short, hypotheses of social selection for unaggressive partners are challenged by the predictable success of a tyrant using brute force for personal gain. The only obvious solution would be that the tyrant is constrained by coalitions that can physically rein in his power, similar to the solution for social selection by female mate choice. The necessity of coalitions goes beyond the normal discussions of social selection, and is considered below (8) and (9).

(5) Self-Control

In primates, absolute brain size predicts neuron number and is strongly correlated with the ability to inhibit prepotent responses (MacLean et al., 2014). Based on the latter finding, Hare (2017) suggested that self-domestication could be promoted by an increased ability for self-control leading to less use of reactive aggression. This idea attributed increased self-control to an incidental consequence of a rise in body size and a concomitant rise in brain size. The rise in body size could have occurred for a variety of reasons.

Hare (2017) considered that the self-control hypothesis conforms to an interpretation of the allometric relationship between brain size and body size that sees human brains becoming notably large as late as 500,000–600,000 years ago. Even such a late date, however, fits awkwardly with the origin of *H. sapiens* around 300,000 years ago.

The self-control hypothesis has been suggested to be a factor promoting self-domestication rather than being a prime mover (Hare, 2017). It is challenged by the problems of why the *sapiens* lineage took a different course from other *Homo*, and by the problem of how increased self-control would lead to selection against domineering behaviors. A classic primate-type alpha male might have excellent self-control but would still benefit by reacting aggressively to any threats to his high status.

Increasing self-control is therefore likely to be relevant as a contributor to the social dynamics of a self-domesticated species more than as a selective pressure against reactive aggression.

(6) Cooperative Breeding

Burkart et al. (2009), Hrdy (2009), and Burkart and van Schaik (2016) proposed that cooperative breeding, a social system in which individuals help rear others' offspring at a cost to their own reproductive effort, became an important feature of early *Homo* society and selected for increased social tolerance. Increased social tolerance implies a reduced propensity for reactive aggression. Regardless of its general merits, with respect to the loss of aggression in *H. sapiens* this hypothesis incurs two kinds of difficulty.

First, the argument made by Hrdy (2009), Burkart et al. (2009), and Burkart and van Schaik (2016) is that cooperative breeding was a feature of the genus *Homo* from *H. erectus* onward, close to 2 million years ago. Their proposal therefore has no special claim on events surrounding the evolution of *H. sapiens* around 300,000 years ago: it does not help explain the evidence that *H. sapiens* underwent a singular form of self-domestication not experienced by other *Homo* species. This problem applies also to Tomasello's (2016) invocation of cooperative breeding as a possible source of reduced aggressiveness, since he accepted the same timing for the evolution of cooperative breeding.

Second, the cooperative breeding hypothesis is concerned mainly with assistance in child-rearing, rather than the control of aggression. While cooperative breeding could in theory promote social tolerance toward infants, juveniles, and mothers by alloparents such as grandparents, sisters and fathers, in practice the propensity for male reactive aggression varies widely in cooperatively breeding mammals. Male-male relationships in tamarins *Saguinus* spp. are especially tolerant, with little evidence of a dominance hierarchy among polyandrously breeding males (Garber et al., 2016). In wolves *Canis lupus* by contrast, a clear dominance hierarchy exists among adults, and male aggression is frequent (Cafazzo et al., 2016).

The idea that cooperative breeding emerged around the start of the Pleistocene means that in theory it might help explain the evolution of a reduced aggressiveness generally in the genus *Homo*. Whether humans are cooperative breeders, however, and what social or cognitive effects cooperative breeding might have had on humans, remain debated (Bogin et al., 2014; Thornton and McAuliffe, 2015; Thornton et al., 2016). Critically, the cooperative breeding hypothesis has not yet been proposed in a way that would explain the reduction of reactive aggression specifically in *H. sapiens*.

(7) Population Density

Cieri et al. (2014) proposed that increasing population density around 200,000 years ago could have been responsible for selection pressures against reactive aggression. They suggested that because higher population density could have increased the pressure to exploit resources controlled by other humans, it would have selected for increased social tolerance toward unfamiliar individuals, an extension of social networks, and more sharing of acquired foods. Marean (2015) developed a similar scenario.

In favor of this general kind of idea, increasing population density was plausibly associated with the cultural developments reported by Brooks et al. (2018) around 300,000 years ago. In experimental studies with captive primates, population density is sometimes associated with reduced aggression and increased tolerance (Aureli et al., 2000). There is also some correlational support from studies of rodents, lizards and birds living on islands. Island populations tend to live at higher density than their continental relatives, and also to show low levels of aggression (Stamps and Buechner, 1985).

On the other hand, genetic data indicate that effective population size of *H. sapiens* fell from 200,000 years ago to 50,000–30,000 years ago, suggesting a mismatch between cultural development and population density (Steele and Weaver, 2014). Furthermore among wild monkeys and apes there is no evidence for an association between population density and social tolerance (Wrangham, 2014); and experimental studies of captive primates show that high population density can lead to an increase in the rate of aggression, or can have no effect (Cordoni and Palagi, 2007; Crast et al., 2015). The population density hypothesis also fails to detail any process responsible for selection directly against alpha-male-style behavior.

The influence of increased population density thus has no clear support at present.

(8) Use of Lethal Weapons

Gintis et al. (2015) addressed directly the problem of how "the standard social dominance hierarchy of multimale/multifemale primate groups" might have been replaced in Pleistocene *Homo* by an egalitarian system, and concluded that the critical factor was the use of lethal weapons. Their key idea was that lethal weaponry, possibly with stone tips, enabled coalitions of individually subordinate males to exert increased control over alpha males by killing them far more easily than before. A shift from hand-held to projectile weapons could have played a role. As a result, the development of advanced weaponry gave power to the disadvantaged, reduced the benefits of individual fighting prowess, and "transformed human sociopolitical life" (Gintis et al., 2015: 327). Similar arguments were made by Woodburn (1982), Bingham (2001), Okada and Bingham (2008), Boehm (2012), Phillips et al. (2014), and Chapais (2015).

Since alpha-males would have maintained their position by reacting violently to challengers, this hypothesis has the merit of suggesting that the use of lethal weapons would lead to selection against reactive aggression. Lethal weaponry would also have facilitated executions. The idea that it was responsible for human self-domestication faces at least three problems however.

First is the timing: documentation of lethal weapons is awkwardly early. Well-balanced fire-hardened spears considered to have been throwable are in evidence at Schöningen by at least 400,000 years ago (Thieme, 1997). Dangerous weapons were likely used much earlier given evidence of hunting. Oldowan stone manuports were possibly lethal throwing weapons in the Lower Pleistocene (Gintis et al., 2015).

Second is the specificity. The hypothesis appears to be as applicable to various other *Homo* who apparently used lethal weapons, including *H. heidelbergensis* and *Homo neanderthalensis*, as it is to *H. sapiens*.

Third, in many species coalitions can kill without using weapons. Lions, wolves, spotted hyenas *Crocuta crocuta* and chimpanzees can kill adult conspecifics at very little risk of injury to themselves (Wrangham, 2019). Humans too can execute victims without using hunting weapons, for example by hanging, burning, drowning, beating, or throwing off a precipice (Otterbein, 1986). Gintis et al. (2015) noted that chimpanzees that attack neighbors for as long as 20 min sometimes do not kill them, but the fact that they sometimes do not dispatch their victims seems less important than that they often succeed in killing (Wilson et al., 2014).

In sum, the use of lethal weapons was probably widespread from *H. erectus* onward, and would have facilitated the deliberate killing of conspecifics. Weapons seem unlikely to have been an important influence on the differences in selective regime between *H. sapiens* and other species of *Homo*, however.

(9) Language-Based Conspiracy

Like Boehm (1999, 2012) and Gintis et al. (2015) proposed that the shift from a typical primate style of alpha-male dominance to the egalitarian male hierarchy of mobile hunter-gatherers depended on males forming coalitions that enabled them to dominate the original alpha. This argument has its roots in a rich literature on the leveling mechanisms that maintain egalitarianism in small-scale society (Boehm, 1993). Even among contemporary self-domesticated *H. sapiens* individual males occasionally try to use their fighting prowess to dominate a group (Boehm, 1999). If such a would-be despot resists being controlled by mechanisms such as ridicule, reprimands or ostracism, he may be executed. Sufficient execution of Pleistocene despots would have led to selection against reactive aggression (Wrangham, 2018, 2019).

Henrich (2016) has argued in similar fashion that "human communities domesticated their members" (p. 188) when violators of social norms were subjected to an escalating series of sanctions, ending in execution. While Henrich did not directly address the decline of reactive aggression, he stressed that the domestication process depended on the evolution of a norm psychology, including an awareness that there are social rules.

An important feature of executions is that they can be planned using proactive aggression. This means that the executioners arrange to kill a victim in a circumstance in which fighting back is essentially impossible. As a result, the killers incur very low costs. The archetypal execution, according to the language-based conspiracy hypothesis, involves killing (by proactive aggression) a male who used reactive aggression to attempt to dominate any challengers to his social power (Boehm, 1999, 2012). The fact that proactive and reactive aggression involve different neurobiological mechanisms means that under a selective regime of alpha males being executed, the propensity for proactive reaction can remain high while the propensity for reactive aggression declines over evolutionary time (Wrangham, 2018). This scenario is supported by the fact that capital punishment has been recorded among mobile hunter-gatherers in every continent, and that aggressive bullies are a common type of victim (Boehm, 2012).

The ability to conduct planned executions means that the killers must share explicit intentions with each other, a capacity that is unique to humans (Tomasello, 2016). Chimpanzees cannot communicate to others that they wish to kill a particular individual, let alone justify their desire, find out if their partner feels the same way, or plan to meet at some future time at a specified place in order to carry out the deed. Those kinds of ability depend on a sophisticated form of language (Wrangham, 2019).

For those reasons, language-based conspiracy appears to be a vital prerequisite for controlling a would-be despot in a mobile hunter-gatherer society, and seems likely to have been equally important in the past. The prediction made by this hypothesis is that linguistic ability was significantly more sophisticated in *H. sapiens* than in *H. neanderthalensis* or other *Homo* species. That idea is plausible (Tattersall, 2016), though hotly debated (Dediu and Levinson, 2013). Further comparison of correlates of linguistic sophistication between *H. sapiens* and *H. neanderthalensis* will provide a helpful test. Quantitative tests of the rates of execution required to achieve the observed phenotypic changes would also be valuable. Unfortunately, however, the ethnographic record of capital punishment is thin: the practice has tended to disappear very rapidly.

In sum, the language-based conspiracy hypothesis can explain why reactive aggression would have been selected against, why this occurred only in *H. sapiens*, and (given that capital punishment was recorded into contemporary times among mobile hunter-gatherers) why reactive aggression has continued to decline. Against this hypothesis, the ethnographic evidence is vulnerable to the difficulty of testing the rate of execution of reactive aggressors.

DISCUSSION AND CONCLUSION

This article is a first attempt to reconcile the anatomical evidence for self-domestication in *H. sapiens* with multiple theories about the evolution of prosocial and antisocial tendencies. It argues that explanations for reduced reactive aggression need to be more focused than ideas about the evolution of human social behavior have typically been. Attention should be paid specifically to evolution in the last 300,000 years, because a critical problem is why *H. sapiens* evolved signals of a reduced propensity for reactive aggression, while other *Homo* species did not.

The conceptual framework assumes that the anatomical signal of a domestication syndrome in *H. sapiens* is a reliable indicator of reduced reactive aggression. Against this idea, across species the precise composition of domestication syndromes is unpredictable, a fact that undermines confidence in using them to infer selection against reactive aggression; and the biological mechanisms responsible for producing domestication syndromes are uncertain (Sánchez-Villagra et al., 2016; Sánchez-Villagra and van Schaik, 2019). Thus the conclusion that *H. sapiens* acquired its current low level of reactive aggression during the last 300,000 years can still be challenged on the basis that the supposed domestication syndrome has resulted from a series of independent adaptations unconnected with the reduction of aggression, and that reduced aggressiveness reflects only an earlier, genus-wide adaptation (e.g., Hrdy, 2009).

Nevertheless, no other selective pressures are known to produce a domestication syndrome, and the resemblances that humans show to domesticated animals include physiological, behavioral and cognitive traits in addition to reduced aggression and a derived anatomy (Hare, 2017; Wrangham, 2019). Furthermore a biological hypothesis for the production of domestication syndromes (Wilkins et al., 2014) has received important support (Wilkins, 2017; Pendleton et al., 2018), including evidence that genetic variants underlying self-domestication occur in *H. sapiens* but not in *H. neanderthalensis* or Denisovans (Theofanopoulou et al., 2017). Similar tests should eventually resolve lingering uncertainties about the meaning of the apparent domestication syndrome of *H. sapiens*. For these reasons the hypothesis that *H. sapiens* has indeed undergone persistent selection against reactive aggression seems strong enough to warrant attempts to explain it (**Table 1**).

Two of the explanations examined were high level theories, i.e., (1) genetic group selection and (2) group-structured culture selection (GSCS, also confusingly called cultural group selection). Both have been applied to the problem of why humans combine exceptionally prosocial behavior within groups with intense hostility between groups: genetic group selection has provided the theoretical basis for the parochial altruism hypothesis, and GSCS for the tribal instincts hypothesis. Proponents of these ideas did not pay particular attention to the problem of selection against reactive aggression, but questions of how and why the propensity for reactive aggression was reduced are closely related to the problems of prosociality with which the two hypotheses are concerned. I therefore considered whether they could account for reduced reactive aggression in *H. sapiens*. I concluded that they do not do so in their current form, partly because in humans, and other primates, effective intergroup conflict is not necessarily associated with reduced within-group aggression. The group selection argument for parochial altruism also does not explain behavioral differences between humans and chimpanzees; and the culture selection argument for tribal social instincts is challenged by the origin of *H. sapiens* being so early that the requisite cultural abilities may not have been present. Other ideas that use group selection or GSCS may prove more promising. For example GSCS could have been involved in the spread of group-based norms for the capital punishment of excessive aggressors [Henrich, 2016, (9)].

Two explanations relied on social selection, respectively, involving individual choice of (3) unaggressive mates and (4) unaggressive task partners. In groups that have egalitarian male dominance hierarchies both ideas are plausible influences on the reduction of reactive aggression. In groups with primate-style alpha males, by contrast, I conclude that on their own these styles of social selection cannot have evolutionary effects. The problem is that a sufficiently aggressive male can achieve his goals even in the face of females or males choosing not to partner with him, as is routinely seen in non-human primates. Coalitionary support is needed to enable partner choice to be effective, but coalitionary support has not featured to date in the social selection hypotheses. Somewhat similar problems apply to the self-control hypothesis (5), which similarly lacks a mechanism responsible for selecting against successful alpha-male behavior.

The cooperative breeding hypothesis for human social evolution (6) could in theory account for reduced aggressiveness, although the evidence for cooperative breeders being unaggressive is inconsistent at best. To date, however, the cooperative breeding hypothesis has been applied to many *Homo* species, rather than specifically to *H. sapiens*, so in its current form it is not a candidate for explaining recent self-domestication.

Increasing population density (7) is associated with reduced aggressiveness in island species, and could in theory play a role in *H. sapiens*' self-domestication. Current evidence about the evolutionary history of human population density, however, undermines any easy correlations, and the relationship between population density and rates of aggression in primates is inconsistent. Studies of causal mechanisms may prove helpful by specifying the conditions in which increased population density leads to reduced reactive aggression (Crast et al., 2015).

The final two explanations were concerned with the use of coalitions to control aggressive males, with the idea that such control could lead to selection against aggressive tendencies. Lethal weaponry (8) has undoubtedly played an important role in human life. However, it does not appear to be associated with *H. sapiens* as tightly or as uniquely as theory would demand, since it has likely been used for a long time before the evolution of *H. sapiens*, as well as in other species of *Homo*. As for language-based conspiracy (9), the time when language became sufficiently sophisticated that subordinate males could confidently plan to kill a better fighter is speculative. We can be confident, however, that the ability to devise shared plans is a rubicon for predictably being able to control physically powerful alpha males who can only be defeated by coordinated action. Language-based conspiracy is not present in chimpanzees: subordinate chimpanzees cannot plan premeditated take-downs of alpha males, which probably partly explains why there has apparently been no selection against reactive aggression in this species. In humans, by contrast, groups conspire against resented tyrants: in mobile hunter-gatherers plans are made and tyrants are executed. This system can plausibly account for selection against reactive aggression occurring only in *H. sapiens*, as Boehm (1999, 2012) has argued.

The language-based conspiracy hypothesis leaves unanswered the question of why language reached the necessary level of sophistication when it did, and why it did so in only one lineage of *Homo*. The simplest possibility is that in the ancestors of *H. sapiens* the appropriate linguistic skills were acquired independently from the control of aggressive behavior (Wrangham, 2019). With weapon use already in place, capital punishment would have been relatively easy. Once reactive aggression started to be selected against, expected effects would have included, as a by-product, increased social tolerance and improved abilities to communicate and cooperate (Hare, 2017). Linguistic skills would probably then improve also (Benítez-Burraco et al., 2018). Thus after the selective system had been initiated, there would likely have been a positive feedback loop leading to an accelerating evolution of traits associated with domestication, as the fossil record seems to indicate (Cieri et al., 2014). The evolutionary decline of reactive aggression would have opened increasing possibilities for social selection and self-control to contribute to the development of prosocial tendencies.

An alternative proposal for language evolution is that linguistic ability increased significantly only after the self-domestication process had been initiated (Hare, 2017). In that case, the language-based conspiracy hypothesis would be inadequate for explaining the origin of *H. sapiens*, and a different stimulus would be needed to account for the early stages of self-domestication.

In sum, among the nine proposals reviewed, the explanation that best accounts for a novel selection pressure leading to a reduction in reactive aggression starting around 300,000 years ago is the emergence of collective intentionality in the form of language-based conspiracy. The evolution of this newly sophisticated cognitive ability would have led subordinates to socially select against aggressive fighters, creating a reverse dominance hierarchy. The spread of the new style of hierarchy could have occurred by individual learning or by selection of group-cultures, and would have paved the way for diverse selection pressures, as shown in **Table 1**, to additionally influence the evolution of the characteristically human social traits.

AUTHOR CONTRIBUTIONS

RW wrote the manuscript.

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By Reverence, Not Fear: Prestige, Religion, and Autonomic Regulation in the Evolution of Cooperation

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Recent evolutionary theories of religions emphasize their function as mechanisms for increasing prosociality. In particular, they claim that fear of supernatural punishment can be adaptive when it can compensate for humans' inability to monitor behavior and mete out punishment in large groups, as well when it can inhibit individuals' impulses for defection. Nonetheless, while fear of punishment may inhibit some anti-social behaviors like cheating, it is unlikely to motivate other prosocial behaviors, like helping. This is because human physiology has evolved separate neurological systems with differential behavioral correlates either for (1) processing fear and responding to threats or (2) facilitating social interactions in environments which are deemed safe. Almost all vertebrates possess autonomic pathways for processing threats and fear, which result in "fight," "flight," or "freeze" responses and so likely mediate interactions in dominance hierarchies. Mammals, however, possess an additional, phylogenetically newer, pathway dedicated to suppressing such defensive responses in the service of promoting social affiliation or engagement. Here, we argue that this mammalian physiology supports an alternative hierarchical system unique to humans: prestige. In contrast to dominance, which involves aversion, fear and shame, prestige hierarchies are characterized by physical proximity and eye-contact, as well as emotions like admiration and respect for leaders. Prestige also directs the flow of cultural information between individuals and has been argued to have evolved in order to help individuals acquire high quality information. Here, we argue that not only does the mammalian autonomic pathway support prestige hierarchies, but that coupled with prestige biased social learning, it opens up a means for prestigious figures, including deities, to support the spread of prosocial behaviors. Thus, in addition to theories that emphasizes religious fear as a motivating factor in the evolution of prosocial religions, we suggest that reverence – which includes awe and respect for, deference to, admiration of, and a desire to please a deity or supernatural agent – is likely just as important. In support of this, we identify cases of religions that appear to be defined predominantly by prestige dynamics, and not fear of supernatural punishment.

Keywords: autonomic nervous system, evolution of cooperation, prestige, dominance, evolution of religion, cultural evolution

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Awe, unlike fear, does not make us shrink from the awe-inspiring object, but, on the contrary, draws us near to it.
(Heschel, 1976)

Be imitators of me, as I am of Christ.
-1 Corinthians 11:1:

The Guru is the conveyance in which the spiritual influence is brought to you. Anyone can teach, but the spirit must be passed on by the Guru to the Shishya (disciple), and that will fructify.
(The Complete Works of Swami Vivekananda, 1895)

GENERAL INTRODUCTION

In recent years, evolutionary explanations of religion have proposed that omniscient, moralizing gods can facilitate cooperation by inducing fear among people and threatening them with punishment for their transgressions (Norenzayan, 2013; Johnson, 2015; Norenzayan et al., 2016; Purzycki et al., 2016). Indeed, gods have been and are feared, but historical accounts and contemporary religious practices show that supernatural agents (gods and saints) and their human representatives (such as priests, gurus, and martyrs) are also profoundly esteemed, adored, loved, respected, awed, freely deferred to, and imitated: in short, they are revered. Revered agents are also often described as being generous and prosocial. In turn, this may inspire a significant amount of generosity and prosociality among their followers without fear.

The goal of this manuscript is to advance a specific hypothesis about the evolution of human prosociality. By prosociality, we mean both norm-abiding behaviors and also costly cooperative behaviors like helping and sharing. Our hypothesis is that benevolent supernatural agents and their human representatives may be as effective at promoting prosociality as fearsome gods. This hypothesis is relevant to self-domestication because this path to prosociality is only possible in humans due to the evolution of prestige psychology in response to our constructed cultural environments. Prestige psychology itself may rely on the evolved structure of the mammalian autonomic nervous system (ANS). Furthermore, unique human modifications to the ANS compared with other mammals may have evolved in response to human cultural practices.

This paper is presented in four sections. First, we will outline the key differences between prestige and dominance hierarchies among animals and humans. Second, we will explain the structure and evolution of the mammalian ANS and how it influences social relationships, especially within prestige and dominance hierarchies. Third, we will discuss how the presence of gods and supernatural agents in both prestige and dominance hierarchies can lead to prosociality. Finally, we will present examples of prestige across religions as well as a focused case study of prestige-driven religious change in the first few hundred years of Christianity under the Roman empire.

DOMINANCE AND PRESTIGE

In dominance hierarchies, individuals often use their strength to threaten and coerce others and gain preferential access to mates and food. Among primates, relative rank is established between members of the same sex and collective awareness of the hierarchy shapes social behavior. Some adult male chimpanzees use intimidation and force to obtain and sustain their dominance status, including agonistic behavior like charging displays (Simpson, 1973; Bygott, 1979) and contact aggression (Watts, 2000a,b; De Waal, 2007), while other male chimps garner support from others over time by grooming them and in turn receive coalitionary support during physical fights in rank contests (Foster et al., 2009). In baboons, high-ranking females have access to the best feeding sites and can keep others away from these sites (Boyd and Silk, 2015) and higher-ranking females have been observed to take in 30% more food than lower-ranking females (Barton and Whiten, 1993).

Rank in dominance hierarchies is associated with fertility among several non-human primates including female chimpanzees, baboons, macaques, gray lemurs, marmosets, and tamarins (Dunbar and Dunbar, 1977; Dietz and Baker, 1993; Digby, 1995; Pusey et al., 1997; van Noordwijk and van Schaik, 1999; Radespiel and Zimmermann, 2001). This is true for other mammals as well: both high-ranking male and female hyenas have increased feeding time at carcasses; high-ranking females have more offspring who survive to maturity, and high-ranking males have more mating opportunities (Owens and Owens, 1996). Females are often aggressive with other females. Amongst naked mole-rats and meerkats, females will fight each other following a dominant breeder's death to win her place (Reeve and Sherman, 1991; Clutton-Brock, 2007). When dominant female meerkats are pregnant, they will antagonize subordinate pregnant females and temporarily evict them from the group, and this stress may result in the subordinate's abortion of the fetus (Young et al., 2006). In addition to mammals, social behavior in dominance hierarchies have been documented in social bees and wasps (Bourke, 1994), fish (Grosenick et al., 2007), and birds (Piper, 1997).

In humans, dominance dynamics include a range of avoidance behaviors. Low-status individuals avoid proximity to dominant individuals, diminish their posture in the presence of dominant individuals, avert their gaze (Henrich and Gil-White, 2001; Henrich, 2016), and raise their vocal pitch (Cheng et al., 2016). Subordinate or low-status individuals may sometimes mimic certain behaviors of dominant individuals, but this is argued to occur only to the extent required to satisfy the dominant and not in cases unmonitored by the dominant (Henrich, 2016). Dominant individuals have more erect posture (Weisfeld and Beresford, 1982) and lower vocal pitch (Cheng et al., 2016) than subordinates; they also are louder, talk more often, and interrupt others more frequently (Octigan and Niederman, 1979; Berger, 2008). Systems of dominance among humans are suggested to be associated with the emotions of shame, fear, and fear-based respect for the dominant, on behalf of low-status individuals (Henrich, 2016).

While dominance hierarchies exist among both humans and non-human animals, only humans possess an additional type of social hierarchy: prestige. Prestige hierarchies are characterized by qualitatively different emotions and behaviors than dominance hierarchies. A prestigious individual is someone who is esteemed for their skill, knowledge, or success in locally valued domains (Henrich et al., 2015). A few examples include: tool-making and tool-use; storytelling, medicine, cooking, and hunting; expertise in rituals, religion, etiquette and social norms; and acquiring wealth. Low-status individuals are likely to show direct gaze toward and desire to be near prestigious individuals, and they demonstrate "preferential, automatic, and unconscious" imitation of them (Henrich and Gil-White, 2001; Henrich, 2016). Followers/copiers (lower-status individuals) feel admiration, awe[1], and respect – reverence – for the prestigious figure.

Prestigious figures are well-liked compared to dominant individuals who are not liked (Cheng et al., 2013). Rather than using fear-inducing threats to coerce others, prestigious figures gain influence simply by being good at something and valued by others for it; moreover, prestigious individuals show generosity and benevolence toward low status individuals (Radcliffe-Brown, 1964; Henrich and Gil-White, 2001; Henrich, 2016). In exchange for their expertise and generosity, prestigious figures receive "freely conferred deference" from low-status individuals (Henrich and Gil-White, 2001). This means that leaders don't command deference by force, and that followers don't show deference simply to reduce the threat from the leader; rather, followers willingly defer to the leader.

Although evidence for prestige outside our species is virtually non-existent, based on ethnographic observations, prestige dynamics appear to be widespread across human societies. For instance, they have been documented in small-scale, mobile societies in the domains of hunting, shamanic knowledge, oration, and combat (Radcliffe-Brown, 1964; Henrich et al., 2015). In more sedentary societies, the "Big Man" phenomenon has been observed in places like Melanesia where, in addition to skill, wealth and economic production can elevate individuals' status resulting in the attraction of many followers (Sahlins, 1963; Henrich et al., 2015). In turn, followers create more wealth as the "Big Man" influences them and organizes them toward more efficient economic production, creating a surplus which he will share. In this way, the prestige dynamic creates a positive feedback loop of followers and success. In some cases, prestige may take a self-aggrandizing turn and status can become a tool for exploitation and strategic manipulation of followers, but the main component of prestige is simply the initial ability attract and influence followers in the first place (Henrich et al., 2015). In addition to field observations, experimental laboratory studies of prestige dynamics have found that young children were twice as likely to copy an adult model to whom bystanders were attending to versus an adult whom bystanders ignored (Chudek et al., 2012). Experiments with adults have demonstrated that both prestigious and dominant leaders emerge naturally in previously unacquainted groups; both types of leaders were judged as influential, but were ascribed different qualities, such as respected and liked (prestigious leader), or "bossy and pushy" and not well-liked (dominant leader) (Cheng et al., 2013).

The different hierarchical systems of dominance and prestige require different evolutionary explanations. For dominance, it is relatively simple: it arises in a context of competition for resources, where there is variation among group members in their ability to acquire resources in the presence of others (Hawley, 1999). Because individuals are typically more interested in their own success than that of their groupmates, competition arises over resources and reproductive opportunities. This leads to a case where the larger, stronger, or, in some species, better connected individuals use their strength (collectively or individually) to increase their access to such resources. For example, subordinate male chimpanzees may invest in grooming other males over time in order to build bonds with them that will pay off in the form of coalitionary support when they fight the current alpha (Foster et al., 2009). This benefits the strong, at the expense of the weak, but by definition the weak are unable to do much about this and so (provided there are no changes to the relative strengths of individuals or alliances, such as a dominant getting ill) stable dominance hierarchies can emerge. Prestige defies such explanations though, because, as discussed above, the individuals at the top of the hierarchy (i.e., prestigious individuals) typically behave with kindness and generosity toward subordinates, and, moreover, rather than taking advantage of this, subordinates respond positively, showing deference.

Unlike dominance, prestige is unique to our species, and as such its evolutionary explanation must be human-specific too. A current explanation for prestige is that it evolved to solve a new kind of problem that arose alongside the human cultural capacity (Henrich and Gil-White, 2001). Specifically, where there is disparity in knowledge or skill among the members of a group, who should you learn from? In some cases, it may be possible to assess the quality of the information offered by potential models. In such instances we should expect individuals with high quality information to be sought out as demonstrators, and in exchange for this information they may be given preferential access to resources or other benefits, as otherwise there would be little motivation for them to share information (beyond close kin, Fogarty et al., 2011). However, in many cases we can expect it to be difficult and/or costly to accurately assess the quality of information offered by different potential models. It would be generally time-consuming to try out each model's method, and if resources are scarce and/or in themselves costly to obtain, such as the wood and other materials required to build a kayak, then there wouldn't be opportunities for trial-and error. In this case an observer might rely on the behavior of their groupmates; observing who other individuals are copying and using that as a heuristic to identify and adopt the most valuable information.

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[1] We are using "awe" in its contemporary positive sense, not the older sense in which includes notions of fear and dread. The latter definition is now considered obsolete by The Oxford English Dictionary (OED), and the positive definition has been in use for the last 700 years: "From its use in reference to the Divine Being this (i.e., immediate and active fear; terror, dread) passes gradually into: dread mingled with veneration, reverential or respectful fear; the attitude of a mind subdued to profound reverence in the presence of supreme authority, moral greatness or sublimity, or mysterious sacredness." Furthermore, the phrase "to stand in awe of" has transformed over time, from meaning "to be greatly afraid of" to "entertain a profound reverence for" (Awe, 2019).

At this point, selected individuals are no longer being copied as a direct result of their skill or quality as a model, rather they are being copied on the basis of a social consensus that they are highly skilled and so should be copied. It is in this sense that prestige is socially conferred. But what is given can be taken away and so an individual's prestige may wax and wane over time. Because prestigious individuals receive benefits from their groupmates they have a vested interest in maintaining their position, and hence, it is argued, they behave prosocially and generously toward other group members such that both parties see the benefit of the prestige hierarchy (Henrich and Gil-White, 2001; Henrich et al., 2015).

The fact that prestige is socially determined, and not based on direct evaluation of model quality, raises the possibility that prestigious individuals may not actually have the highest (or even high) quality information. While this is certainly a possibility, observers likely do have some information about quality and so prestige is unlikely to be entirely divorced from model quality. Nonetheless, prestige does not need to be perfectly directed to be adaptive. As long as it directs social learning more effectively than it would be otherwise, it will increase fitness and so be favored by selection. This selection will shape human psychology to further entrench prestige hierarchies and prestige-biased copying. The outcome of this is that humans have an adaptive, evolved preference to defer to and copy people of high social status or "who seem generally popular," and this preference yields an improved quality and fidelity of socially-transmitted information (Henrich and Gil-White, 2001). This results in a system where prestigious individuals are continually sought as models and receive many benefits in exchange for their information, such as positions of leadership and access to resources. Thus, prestige systems are not altruistic but rather mutualistic, with low status individuals offering deference in exchange for high quality information. Moreover, this explains why prestige evolved only in humans, since only humans rely on cultural inheritance to the extent that prestige is necessary.

THE HUMAN AUTONOMIC NERVOUS SYSTEM (ANS) AND THE POLYVAGAL THEORY (PVT)

In this section, we outline and review the evidence for the polyvagal theory, a biobehavioral model that relates the functions of the human ANS to behavioral self-regulation and social engagement. We then describe how these behavioral correlates of the human autonomic functioning map onto behaviors which are characteristic of dominance and prestige hierarchies.

Vertebrate nervous systems can be divided into two main parts: the central and peripheral nervous systems (PNSs). The central nervous system (CNS) is situated in the brain and the spinal cord, the latter of which, in large part, carries information to and from the brain. The PNS connects to the CNS and can be further divided into two sub-systems: (i) the somatic nervous system (SNS), which includes nerves that carry motor signals from CNS to skeletal muscles and is associated with the *voluntary* control of these muscles, and (ii) the ANS, which includes nerve connections between internal organs and the brain and is associated with *involuntary* control of bodily processes like breathing, digestion, and heartbeat. The ANS is again divided into two sub-systems: the sympathetic (associated with "fight or flight" responses) and parasympathetic (associated with restoration and growth, or "rest and digest") systems. Where organs are innervated by both the sympathetic and parasympathetic nervous systems, they have antagonistic influences on each other. For example, pupils dilate via the sympathetic ANS, but they constrict via the parasympathetic ANS.

Freezing is a common fear response across species. Freezing helps to avoid detection by predators and can also prepare an animal for action. It entails slowing of the heart rate and it is regulated by the parasympathetic nervous system. It is not simply a passive state, but rather can be thought of as a parasympathetic "brake" on the motor system, temporarily putting sympathetic systems on hold and preparing the animal for further defense responses (including sympathetically-regulated fight or flight) when this brake is released (Roelofs, 2017). It is important to note that during freeze as well as during many other processes, the sympathetic system does not completely shut down or become inactive, but rather it is selectively dampened by parasympathetic dominance. Because of this, heart rate, for instance, is therefore not always an indicator of arousal, since an animal can slow its heart rate via its parasympathetic system even while its sympathetic system remains active, promoting increased awareness and perception. Nonetheless, freezing can lead to tonic immobility or "playing dead" in the cascade of fear responses (Roelofs, 2017).

Mammals exert parasympathetic control of their hearts every time they breath out: during exhalation, the parasympathetic nervous system slightly slows the heart rate. This naturally occurring variation in heart rate during the breathing cycle is called respiratory sinus arrythmia (RSA). On the in-breath, heart rate increases which circulates blood oxygen throughout the body, and on the out-breath, the heart rate slows and energy is conserved. RSA has been widely and almost exclusively observed in mammals (though for a recent example of RSA in lungfish, see Monteiro et al., 2018). Heart-rate deceleration, both during RSA in mammals and during freeze responses in reptiles and mammals, is controlled by the parasympathetic system via the vagus nerve. When RSA is measured, it is a reliable way to assess the parasympathetic innervation of the heart mediated by the vagus nerve (Philips and Donofrio, 2009).

In humans, the vagus is the 10^{th} cranial nerve. It is a bi-directional mixed sensory/motor nerve; that is, it sends motor information from brain to organs, as well as sensory information from organs to brain. The many connections of the vagus form a family of neural pathways. The name, "vagus," is derived from Latin, meaning "to wander" and this name is reflected in the structure of the nerve: it has the longest and widest distribution of any nerve in the body, and provides motor fibers to all organs (except adrenal glands) ranging from the neck to the abdomen, including the throat, ears, heart, lungs, and digestive tract. Indeed, the vagus comprises 75% of all parasympathetic nerve fibers and is the predominant neural effector (Czura et al., 2007).

Porges (2011) proposes that mammals have evolved not one, but two branches of the vagus, a state he refers to as "polyvagal." The branches can readily be identified in mammalian anatomy, develop separately from each other, and are argued to have separate evolutionary origins. While, for the most part, each branch innervates different organs and muscles, they both exert control over the heart, and do so to two adaptive ends: (1) the first branch exerts control over the heart for metabolic conservation (this function is shared with reptiles) and (2) the second branch exerts control over the heart in the service of social behavior (this function is exclusive to mammals). The two different mammalian vagal branches originate in multiple nuclei of the brainstem: (1) the dorsal motor nucleus of the vagus (DVN), and (2) the nucleus ambiguus (NA), a large group of motor neurons (see Taylor et al., 1999 for an extensive review).

Freeze responses in mammals and reptiles follow the phylogenetically older pathway of the dorsal vagal complex (DVC) originating in the DVN. Signals sent along this pathway slow the heart rate during a freeze response. The dorsal branch of the vagus also innervates organs below the diaphragm, serving digestive function; specifically, stimulating increased secretion and motility in the gastrointestinal tract ("Cranial Nerves: Visceral Motor," Patestas and Gartner, 2016). In mammals, the newer vagal branch originating in the nucleus ambiguus (NA) also innervates the heart, as well as several organs and muscles above the diaphragm. Specifically, it supplies fibers motor neurons to the larynx (vocalizations and breathing), soft palette (swallowing and breathing), uvula (gag reflex), and pharynx (vocalizations and breathing), as well as the ear canal (sound transmission), tragus (sound direction/location), and auricle (this visible part of the ear; amplification of sounds). Near this auricular region, it also joins up with the facial nerve (cranial nerve XII). All of these muscles innervated by the supradiaphragmatic vagus are involved in human communication and sociality. The polyvagal theory proposes that the addition of this vagal nucleus in the NA, with its connections to the heart as well as muscles in the neck and face, represents an evolutionary change in the ANS to facilitate social engagement (Porges, 2011). In effect, this newer vagal pathway can be considered to act as a parasympathetic "brake" on hostile or avoidant sympathetic impulses during social interactions.

As mammals with complex social lives, this "brake" is useful to humans because they must be able to balance the activity of their sympathetic and parasympathetic ANS in the service of emotional and behavioral regulation in response to social inputs. An example of this is eye contact, which can be a cue of threat or signal of engagement during communication. Non-human primates engage in eye contact in both agonistic and affiliative behaviors. Among rhesus macaques, staring frequently co-occurs with threatening vocalizations toward conspecifics (Partan, 2002). Different species also show divergent preferences for the amount of eye contact in general: bonobos, who are more affiliative and less aggressive than chimpanzees, show more of a preference for facial characteristics (eyes, mouth) of conspecifics versus other body parts compared with chimpanzees (Kano et al., 2015). In keeping with this, studies with human adults find that attention to eyes increased in both affiliative and threatening situations (Kleinke, 1986; Emery, 2000). Similarly, preferential attention to eyes emerges early in human development, with infants preferentially looking at faces that engage them in mutual gaze (Farroni et al., 2002). A parasympathetic "brake" when eye contact is made would be necessary for facilitating positive social interactions. When parasympathetic activity is lacking, people may overinterpret the threat of eye contact and/or they may avert their gaze. Among human adults, for example, gaze fear and avoidance are common among those with social anxiety disorder, a disorder which involves the intense anxiety or fear of being judged, negatively evaluated, or rejected in a social situation (Social Anxiety Disorder, 2010–2018; Schneier et al., 2011; Weeks et al., 2013).

The ability to distinguish human voices from other sounds is also important in human social interactions. The auricular branch of the vagus can trigger an involuntary contraction of the middle-ear muscles, known as the acoustic reflex. The acoustic reflex occurs immediately before a person starts to speak or when other people are speaking and serves to selectively amplify perception of human vocalizations by decreasing the sensitivity of the ear to low-frequencies. **Table 1** shows the different ANS responses which have been described so far, along with examples of corresponding muscles/organs and behaviors resulting from these responses.

One of the main ways the vagus mediates social behavior is by promoting calm states, and this is done through control of the heart. Healthy individuals exhibit parasympathetic control of their heart via the vagus during breathing. This phenomenon is known as RSA, the natural covariation between respiration and heart rate. RSA is believed to occur in order to increase the efficiency of the exchange of oxygen and carbon dioxide between the alveoli (via ventilation) and pulmonary capillaries (via perfusion/blood circulation) (Yasuma and Hayano, 2004). RSA is an index of parasympathetic – specifically, vagal– control of the heart. Under resting conditions, healthy individuals exhibit periodic variation in the length of time between each beat of their heart (R-R or inter-beat intervals measured during an electroencephalogram or ECG) during breathing (Shaffer and Ginsberg, 2017). The measurement of inter-beat intervals allows quantification of heart-rate *variability* (HRV). In general, exhibiting HRV during a resting state is a sign of good vagal tone and suggests an individual should be able to recover more quickly (i.e., slow down their heart rate) from a stressful stimulus than someone who has low or poor vagal tone. In other words, good vagal tone as HRV equates to increased parasympathetic activity and the ability of the individual to quickly "switch gears."

Research using RSA methods have shown that healthy vagal tone is associated with human social engagement and self-regulation (Geisler et al., 2013), including the capacity for sympathy among children (Taylor et al., 2015) and compassionate responses toward others' suffering (Stellar et al., 2015). Poor vagal tone is associated with health problems including preterm, high-risk infants (Shinya et al., 2016), and anxiety disorders in adults (Chalmers et al., 2014), including military combat veterans with post-traumatic stress disorder (PTSD)

TABLE 1 | Bio-behavioral correlates of autonomic neurological structures.

ANS response	System	Associated organs/muscles	Behavior/function
“Freeze”	Parasympathetic: “vegatative” vagus via the dorsal vagal complex (DVX)	Heart-rate deceleration (neurogenic bradycardia)	Metabolic conservation Immobilization, potential tonic immobility (death-feigning)
“Flight” or “Fight”	Sympathetic	Heart-rate acceleration Eyes, etc.	Mobilization: fleeing away or aggression. Pupil dilation, etc.
Social engagement system and “immobilization without fear”	Parasympathetic: via the evolutionary newer “ventral vagal complex (VVC)”	Heart-rate deceleration Middle ear muscles	Increased vagal tone measured by RSA (respiratory sinus arrythmia) Selective amplification of human vocalizations over other sounds; listening
		Striated muscles of the face and neck	Facial expressions, head turning
			“Emotional” cueing of the eyes, eye contact
			Head turning and tilting
		Pharynx and larynx	Prosody in speech
		General social engagement system	Quiescient social states: conception, nursing, physical proximity to others, etc.

Modified from Lenfesty and Fikes (2017b) *after* Porges (2011).

(Jovanovic et al., 2009) and victims of childhood abuse and neglect (Dale et al., 2009). The causal relationship between RSA and behavior is complicated though, and socialization has been found to improve vagal tone among people who are depressed (Schwerdtfeger and Friedrich-Mai, 2009).

The polyvagal theory argues that the mammalian ANS has evolved two vagal pathways which, when activated, have different behavioral outcomes. The first pathway functions to process threat and fear and elicits a “freeze” defense response which slows of the heart via the DVC, a pathway that mammals share with reptiles. The second parasympathetic pathway also regulates the heart via the vagus, but in addition innervates muscles in the head and neck. This pathway functions to support calm states and human prosocial interactions, including communication.

The stimuli and behaviors which correspond with the activation of the two vagal branches of the mammalian ANS map on well to what we observe in dominance and prestige hierarchies. We expect that the fear and threat that dominant individuals wield (including fear of and threat of punishment, supernatural or otherwise) are processed by receivers via the evolutionarily older DVC. This prepares receivers to submit and do nothing (shut down or freeze) or prepare to take action (flee or fight the dominant). In contrast, we expect that prestige-biased transmission involves the activations of newer vagal pathways which enable individuals to calmly engage with and pay attention to the prestige figure in order to learn from them by listening, communicating, observing, and making eye contact with them without either party inferring a threat or challenge. And while many non-human mammals, including primates, exhibit the kind of social engagement or affiliative behaviors expected from the phylogenetically newer vagal pathways – such as nursing, grooming, bonding, huddling, non-aggressive proximity or physical contacts – they lack prestige, so there is no synergy between these autonomic processes and prestige-biased social learning. We expect that in humans, healthy functioning of the newer ANS pathways supports and interacts with prestige dynamics to produce a bulk of cooperative behaviors that cannot be produced by fear-responses in dominance hierarchies. We will now turn our focus toward how prestige and dominance hierarchies and their complementary autonomic pathways can (or cannot) support the evolution of prosocial behaviors, particularly in the context of religion.

TWO PATHWAYS TO COOPERATION

Before addressing the possible range of cooperative behaviors possible for humans given our evolved physiology (ANS) and evolved social structures (dominance and prestige), we will briefly summarize just how prosocial we are as a species. If domestication is the process by which other species came to live alongside our own, then human self-domestication is, in part, the process by which humans became remarkably more collaborative with conspecifics. Indeed, compared to any other vertebrate species, we are far more cooperative. Humans help others through alloparenting (Hrdy, 2011; Bentley and Mace, 2012), caring for the sick and needy, and supplying and/or building public goods. Human cooperative relationships are frequently based on reciprocity in which behaviors are tracked and exchanges are delayed (Trivers, 1971; van Veelen et al., 2012). Humans are “ultrasocial,” but this ultra-sociality is puzzling in that it is not explained through genetic relatedness (Mathew, 2015). Humans frequently interact with and cooperate with non-kin, and, compared with other species, this is highly unusual if not completely unique (but see West et al., 2011, for criticism). Given this, the scope and evolution of human cooperation has been a major focus of study for several decades. Here we will explore the potential roles of dominance and prestige, as well as cultural evolution, in this process.

The ability of dominance to foster cooperation must be limited. Indeed, if it were not then it would be hard to explain why cooperation like that of humans is so rare while dominance hierarchies are widespread across species. Nonetheless it is important to understand why this is the case. First let us consider how dominance might support cooperation: when the dominant individual demands it of their subordinates, and punishes those who disobey. If a low-ranking individual defects, they may be punished by higher-ups, and so cooperation may be somewhat stable through coercion. But what if it is a high-ranking individual that defects? Indeed, there is little to stop dominant, selfish individuals exploiting cooperators while not being cooperative themselves. As such, the kind of cooperation fostered by a dominance hierarchy is very different to that observed in human behavior. This is indeed what we observe in many non-human species as discussed above; dominant individuals force subordinates to behave "cooperatively" (i.e., in the interest of the dominant). So, subordinates behave cooperatively, but dominants are selfish.

However, even the ability of dominants to enforce cooperative behavior among subordinates may itself be limited because dominant individuals can enforce cooperative behavior only when they are present. When absent, a leader would have to rely on a loyal network of minions to monitor and enforce behavior of subordinates. This, however, creates the problem of second-order free-riders who could possibly defect on carrying out punishment. Given this, as group sizes grow larger, it would become impossible for a leader to monitor all behavior and so the attempts of dominant individuals to enforce cooperation amongst subordinates cannot be entirely successful.

Dominance as a mechanism for sustained cooperation is thus limited. One solution to the problem of both first- and second-order free-riders in large groups is punishment from moralizing, omniscient, "Big" gods (Norenzayan, 2013; Norenzayan et al., 2016; Purzycki et al., 2016). Under the Big Gods hypothesis, supernatural agents who are believed to monitor behavior and punish transgressions are an effective way of supporting cooperation in large groups. Johnson (2015) makes a similar argument that belief in supernatural punishment can support cooperation, but that it primarily provides individual-level fitness benefits: since individual selfish behavior can be costly, belief in supernatural punishment can inhibit individuals' selfish impulses and thus save them the cost of being punished by other people (so long as punishment from others is present and efficacious in that individual's social network). Regardless of the level(s) of selection upon which supernatural punishment operates, the deity is effectively taking the place of the dominant individual. Fear is key to these hypotheses. Believers must actually fear the god(s) and believe that they will be punished if they transgress a norm. In this way, fear of punishment is supposed to curb anti-social behavior and gods are like dominant leaders: they wield their influence through intimidation and force, and followers submit to them out of fear. Note that this solves the two problems with dominance supporting cooperation: (1) the deity is assumed to be omniscient and so the issue of monitoring disappears, and (2) the deity is not perceived to be dependent on humans and therefore has no incentive to be tempted into defection because there are no benefits for the deity to reap. Of course, in human societies specific individuals are often assigned the role as being a spokesperson for the deity and so such conflicts of interest will likely re-emerge.

While supernatural punishment accounts of the evolution of cooperation are viable, here we present an alternative that relies on systems of prestige instead of dominance. As already discussed, the existence of prestige-biased learning implies that followers copy traits from prestigious leaders; if in addition to being skillful/knowledgeable prestigious leaders are also cooperative (as they are often described as being), and if followers imitate more of the leaders' traits than just the target trait (i.e., skill, knowledge), cooperativity could spread through the population. Indeed, in a set of culture-gene coevolutionary models, Henrich et al. (2015) found exactly this: that cooperation can be stable even in large groups when cooperativity is a cultural trait that is learned from prestigious leaders and passed on to future generations by followers.

At this point we will make the same step as proponents of supernatural punishment theories of cooperation by invoking gods of our own: while fear of deities and supernatural agents (and even impersonal moralizing forces like karma) may be widespread across cultures, gods and supernatural agents are also revered, admired, adored, respected, and loved. In short, Gods and supernatural agents are prestigious as well as dominant. Rather than using fear of supernatural punishment to promote cooperative behaviors, prestigious gods/supernatural agents tap into human psychology which is biased toward imitating prestigious individuals to promote cooperation without the need for threatening punishment. Indeed, the spread of cooperation via prestige-biased transmission may not even rely on close monitoring of group members because part of human prestige psychology is an active desire to be like prestigious individuals at all times, and not just in their presence.

In support of a role for prestigious gods, it has been previously argued that fear, and fear of punishment specifically, alone cannot account for the range of observed prosocial behaviors in religions. Lenfesty and Schloss (2015) have encouraged scholars to make a distinction between the mechanisms that simply make people less likely to violate prevailing behavioral norms (i.e., supernatural punishment), and what makes them "nice." Johnson and Cohen (2016) have similarly argued that "refraining from doing bad" is not the same as "doing good." Lenfesty and Fikes (2017a,b), after Porges (2011), have proposed that these two categories of prosocial behaviors arise from separate neurophysiological systems. Critically, experiments have shown that different types of prosocial behaviors result from different perceptions of god. For example, Johnson et al. (2013) found that among both Catholics and non-Catholic Christians, people who had predominantly authoritarian concepts of God were more aggressive while those with a predominantly benevolent concept of God were inclined toward volunteerism and showed greater willingness to aid religious out-groups. In another study by Johnson et al. (2013), participants were given reminders of a either a benevolent or authoritarian god; the former type increased the willingness to forgive, while the latter type increased aggression and decreased forgiveness, as well-decreased the willingness to conserve water, volunteer, or aid religious out-groups. While Johnson et al. (2013) did not explicitly use the words "dominance" or "prestige" in their Authoritarian/Benevolent God scale, the majority of their items overlap with experimental, ethnographic, and historical descriptions of traits of dominant and prestigious leaders.

As previously discussed, feeling fear frequently results in a physiological and behavioral "freeze" response, and while freezing may inhibit some antisocial behaviors, it cannot lead to other kinds of social engagement behaviors like helping and caregiving. If gods are predominantly fearmongers, prosocial behaviors will be limited to what only fear can achieve. In order to facilitate approach-driven prosocial behaviors, the environment would have to provide more positive cues that could in turn activate parasympathetically-mediated social engagement behaviors.

Note that our argument is not that dominant deities cannot promote prosocial behaviors, or that proponents of supernatural punishment theories of religion are wrong. Rather, we suggest that there is a second means by which gods can be used to promote cooperation. Cooperation can be demanded by dominant gods who threaten punishment if disobeyed, or it can be requested or inspired by prestigious gods who offer a chance to share in their benevolence if acquiesced to. These should not be viewed as mutually exclusive options, and a carrot-and-stick mix of prestige and dominance may well be the norm. Moreover, different groups within the same religion may emphasize and focus on either the fearful or benevolent aspects of a given deity.

CASES OF PRESTIGE-DRIVEN DYNAMICS IN RELIGIOUS HISTORY

We have now outlined the core of our theory: that prosocial, prestigious gods can tap into human psychology to promote cooperative behaviors in a way that dominant gods cannot because the two types of deities activate different neurophysiological systems. In this final section we will review historical cases that show the effects of prestigious gods in action in order to provide evidence that prestigious gods have been an important part of the evolution of human behavior.

Prestige dynamics can be observed in many religions or spiritual groups where highly revered central figures act as teachers and guides (as opposed to domineering aggressors) who disperse their knowledge and skills to followers who are inclined to imitate their ways. All branches of Buddhism are centered around Gautama Buddha's life and teachings, mainly the Four Noble Truths (i.e., the truth of suffering, the truth of the cause of suffering, the truth of the end of suffering, and the truth of the path that leads to the end of suffering) and the Noble Eightfold Path (i.e., right understanding, right thought, right speech, right action, right livelihood, right effort, right mindfulness, and right concentration). Interestingly, the story of Siddhartha Gautama (a.k.a. the Buddha) involves him renouncing his position within a class of ruling elites (an already prestigious position) and giving up all the wealth associated with it and becoming a monk and traveling teacher. In Hinduism, gurus are literally "ignorance dispellers" (Sanskrit: *gu*, "ignorance," *ru* "dispeller"): highly revered teachers who serve as models and guide students not only in the development of spiritual knowledge, but also the arts (e.g., music and dancing) (Mlecko, 1982). Islam centers around the teachings of the prophets (Noah, Abraham, Moses, Jesus, and most importantly, Muhammad), who model ideal human behavior and are revered as messengers sent by God.

Modern Anglican bishop and theologian Wright (1999) asserts that, historically, Jesus stood apart from the other religious leaders with regard to one event in particular: his alleged resurrection. Historically, the Christian worldview has been centered around escaping death and obtaining eternal life. Jesus may have acquired prestige because his followers believed he was the only person ever to have escaped death through his resurrection, an immensely valuable skill they hoped to share in by following his teachings. To the Jews, death meant a denial of God's good created order and the Hebrew prophets of the Torah predicted a time when God would restore this order (Wright, 1999). The Christians saw Jesus as the restoration of the world order and believed that by having faith in him and a commitment to his values they would receive the same ability to escape death, that is, the promise of eternal life. A cultural evolutionary reading of the Biblical texts portrays Jesus receiving deference from his followers in exchange for his fitness-relevant expertise in the domain of social norms (e.g., the behaviors required to live a moral life, how to navigate life's challenges); the added expertise on how to overcome morbidity and obtain eternal life likely made him even more sought after.

Thus, the role of religious figures as knowledge-bringers (a key part of prestige systems) seems widespread. However, another part of our hypothesis is that prestigious, religious figures specifically advance prosocial behaviors in their flock. While all of the world's major religions and their leaders explicitly teach about almsgiving, charity, and generosity, we focus on here on early Christianity as an example of prosocial behavior emerging from a prestige hierarchy. In the New Testament, Jesus is portrayed as having a group of dedicated followers (i.e., the disciples) who follow him closely and receive direct teachings from him. In artwork depicting Jesus delivering the Sermon on the Mount – a moralistic message and guide for living, including the commandment to love one's neighbors and enemies as well as give to the needy – he is portrayed as sitting or standing only slightly above his disciples and the crowd, with an open body posture of both arms extended to his sides or one had gently raised. These gestures fit with description of prestige displays, which are less expansive than dominance displays (Henrich, 2016).

New Testament texts describing the dynamics between Jesus and the disciples also map onto ethnographic and psychological descriptions of prestige dynamics, including the leader-follower dynamics of "Big Men" societies (Henrich et al., 2015), where highly skilled individuals command respect and exert influence over a group of followers. Like many other leaders, the character of Jesus portrayed in the New Testament appears to be a charismatic and highly skilled orator who had the purported power to perform miracles (i.e., heal the sick, feed the masses), which were received as acts of generosity.

A closer look at the rapid rise of Christianity in its first five centuries reveals how Jesus himself as well as the disciples who went on to preach his gospel (i.e., Paul) were successful not only in accumulating followers on his behalf and advocating for prosociality, but also in promoting prosocial behaviors amongst believers, which in turn further drove the growth of the fledgling religion. In a 260-year period, Christianity rapidly expanded from an obscure Messianic cult movement in the far edge of the Eastern Roman empire to an estimated size of 5–7.5 million members (Stark, 1996). Sociologist Rodney Stark attributes the success of Christianity to several key factors, including the highly prosocial response of Christians to two severe plagues that ravaged the empire between the 1^{st}–5^{th} centuries AD. The Antonine Plague swept through Roman Empire from 165 to 180, resulting in the loss of an estimated quarter to a third of the entire empire's population during the first plague (Boak, 1947; Russell, 1958; Gilliam, 1961; McNeill, 1976). By the end of the second plague, the Plague of Cyprian from 251 to 266, classical society was severely "disrupted and demoralized" (Stark, 1996, p. 74). During this time, Pagan leaders and government officials offered no assistance or care for the sick, while Christianity – still a minor but increasingly growing movement – did.

There is little historical textual evidence to suggest that fear of God was a primary motivator in the nursing practices of Christians in the first five centuries AD. This is because even though Christians faced severe losses, they viewed the plagues as trials of their faith and not as direct punishment from God. Eusebius' history of the early church includes an Easter letter from Dionysius, the bishop of Alexandria, during the plague in 250, in which he writes that "heathens" faced even greater losses because of how terrifying it was to them (p. 240). Dionysisus contrasts the behavior of the two groups:

> Most of our brethren showed love and loyalty in not sparing themselves while helping one another, tending to the sick with no thought of danger and gladly departing this life with them after becoming infected with their disease. Many who nursed others to health died themselves, thus transferring their death to themselves. The best of our own brothers lost their lives in this way – some presbyters, deacons, and laymen – a form of death based on strong faith and piety that seems in every way equal to martyrdom. They would also take up the bodies of the saints, close their eyes, shut their mouths, and carry them on their shoulders. They would embrace them, wash and dress them in burial clothes, and soon receive the same services themselves.
>
> The heathen were the exact opposite. They pushed away those with the first signs of the disease and fled from their dearest. They even threw them half dead into the roads and treated unburied corpses like refuse in hope of avoiding the plague of death, which, for all their efforts, was difficult to escape.
>
> (Maier, 1999, p. 240)

Although it could be argued that Dionysius had a biased view of Christian charity, Harper (2016) makes the point that it would be difficult to exaggerate or fabricate an experience that his audience was experiencing first hand.

There are also pagan accounts of how the responses of the two groups differed. The Christian movement continued to grow after the plagues and by 313 it was enough of a force that the emperor Constantine finally made it a legal religion in the empire with his Edict of Milan. 100 years after the second plague in 362, the Emperor Julian wrote to Arsacius, the high pagan priest of Galatia, with some instructions on how to rescue the waning pagan religion which was severely lacking in the area of public service. Julian ordered Arsacius to basically force other priests to copy what the Christians were doing, and punish them if they did not conform to his orders:

> The Hellenic religion does not yet prosper as I desire. . .. why do we not observe that it is their benevolence to strangers, their care for the graves of the dead and the pretended holiness of their lives that have done most to increase atheism [i.e., Christianity]? I believe that we ought really and truly to practice every one of these virtues. And it is not enough for you alone to practise them, but so must all the priests in Galatia, without exception. Either shame or persuade them into righteousness or else remove them from their priestly office. . .
>
> (Wright, 1913)

Julian saw the need to compete with Christians, who were helping both their fellow Christians as well as pagans. Julian promised to send Arsacius large amounts of food and wine as a way to entice "strangers and beggars," especially, into the pagan religion. But he also used shame to motivate the cooperation of his subordinate, writing:

> For it is disgraceful that, when no Jew ever has to beg, and the impious Galilaeans [i.e., the Christians] support not only their own poor but ours as well, all men see that our people lack aid from us. Teach those of the Hellenic faith to contribute to public service of this sort. . .let us not, [allow] others to outdo us in good works.
>
> (Wright, 1913)

Interestingly, Julian's letter represents a dominant strategy to cooperation: even if the end goal was providing social services, this should be done through use shame and threat of punishment to the "management," i.e., the priests carrying out the services.

Martyrs were also an important source of inspiration to Christian prosocial behavior and an extreme example of what early Christians were willing to give up to benefit their group. Eusebius' *Church History* reports several stories of early Christians being beheaded, burned alive, and tortured. These accounts portray the martyrs as recalcitrant to the Romans even while being tortured. Galen, the famous Greek physician to the imperial court of Rome, was present during the Antonine Plague. Of the resilience and virtue of the Christians, he wrote,

> For their contempt of death is patent to us every day. . .and they also number individuals who, in self-discipline and self-control in matters of food and drink, and in their keen pursuit of justice, have attained a pitch not inferior to that of genuine philosophers.
>
> (Walzer, 1949, p. 15)

Martyrdom likely served two important and related functions during this time of early Christianity. First, it reinforced the Christian belief that death (by martyrdom or disease) shouldn't be feared because they believed that eternal life was possible. For reasons discussed previously, the strengthening of this belief may have damped the amount or degree of fearful states that would have prevented social engagement (helping, communication) among Christians.

Second, martyrdom in early Christianity maps well onto the cultural evolutionary theory that such displays or "CREDS" (CRedibility Enhancing Displays) operate through an evolved social-learning psychology where learners use models' behavior to determine how much to commit to a belief (Henrich, 2009); in this case, the models' behavior is very costly so their credibility is high which strengthens the observers' motivation to buy into the ideology. Henrich's (2009) analytic model shows that the stable presence of CREDS in groups can increase the success and competitiveness of a group by increasing cooperation. This is possible because the CRED (a) is an altruistic act which provides direct group benefits, (b) is an act of punishment that penalizes non-cooperators, and/or (c) delivers no immediate *direct* benefits to the group but elevates and stabilizes an ideology that favors other group-beneficial behaviors (Henrich, 2009). In the case of early Christianity, type (a) CREDS include helping/nursing fellow Christians (plus any pagans who would later convert to Christianity because they were cared for) and type (b) CREDS include martyrdom which would presumably lead to more prosocial behaviors of the (c) type.

These beliefs and behaviors are nested within a religious prestige hierarchy where followers are also motivated to attend to a central figures' (i.e., Jesus') expertise on how to obtain eternal life. The positive feedback loop effect of prestige, where an increase in the number of followers increases the prestige of the prestigious person, which in turn increases the figures' sphere of influence, seems to have been a major part of Christianity's success. This, combined with the CREDS of Jesus himself like healing disease and providing food to the masses, as well as the crucifixion (which was interpreted as an extreme sacrifice, i.e., dying for the sins of humankind), would have increased prosociality within early Christianity. Finally, specifically Christian beliefs that functioned to dampen fear responses in the body would have benefited Christians' social relationships by allowing them to maintain calm autonomic bodily states.

Since the time of its beginnings under the Roman Empire, Christianity has become the most widely practiced religion in the world. Although its practices and theology have widely varied, as seen through the rise, fall, and maintenance of hundreds of denominational sub-groups, examples of prestige concepts are prominent it its modern form. For example, Hillsong Church – a Christian megachurch in Australia with weekly services of over 43,000 with an additional 1.7 million people in other parts of the world linked to a livestream of its service (Hillsong Church Annual Report, 2018) – is a major producer of contemporary Christian music with lyrics that promote a prestige-concept of God and Jesus. Hillsong's worship music-centered YouTube channel has 4.7 million subscribers (as of October, 2019); the lyrics of one popular song, "To Be Like You," say: "I will walk/In Your ways/Love Your word/Seek Your face/My reward/My sole pursuit/To know You more/To be like You/Jesus/All I want is to be like You." The lyrics of another popular worship song by River Valley Worship (YouTube channel with 9.4k subscibers as of October, 2019), "Wanna Be Like You," similarly say: "Come and change my heart/show me who You are/I wanna be like You, I wanna be like You/Take my heart, my soul, I give You control/I wanna be like You, I wanna be like You, Jesus." Grammy-award winning and top Billboard chart-achieving gospel singer Tasha Cobbs Leonard's song, "By your spirit," says: "Not by might/Not by power/By your spirit God/Send your spirit God/You called us out/Out of the darkness/Into your love/Into your light/Grace upon grace/Beauty for ashes/You come to us/We come alive/We stand in awe of you." These are just a few examples of many contemporary worship songs that emphasize the imitation of the traits of supernatural prestigious figures.

Regarding how prestige hierarchies in religion can foster healthy autonomic functioning, and therefore lead to prosocial behaviors, Luhrmann (2012) describes in her ethnography of the popular Vineyard Church how members its members' emotional states and behaviors change as a result of conceptualizing a benevolent and loving god. She writes, "People are told that they are safe and loved. . ..When people feel lovable, they are less likely to interpret a curt tone as an insult. . .the social life of evangelical churches is rich in specific emotional practices. . .these emotional practices create powerful feelings. . .they lead the congregant to want to change and practice the change, [and practice] the experience of being loved by God." We expect that when cultural narratives of benevolent and prestigious supernatural agents are reinforced through collective rituals such as singing, prayer, reading of texts, and listening to sermons, this can create safe environments where positive emotions and behaviors – like the desire to be like a help others – can, as a result of calm autonomic states, thrive.

CONCLUSION

We have described how the phylogenetically older vagal systems that humans share with animals operate to process fear (threats), as well as how dominance hierarchies are characterized by fear and intimidation. Given that humans, like all mammals, have phylogenetically newer vagal adaptations for social engagement which suppress fear responses, and that human social life is characterized not only by dominance but also by prestige dynamics, we hypothesize that such newer vagal pathways function in part to support this alternative social hierarchy of prestige. We therefore expect that cultural traits like prosocial/altruistic religious ideas and practices will capitalize on these systems and spread via cultural evolutionary processes.

The evolution of a prestige psychology in humans opens up a new means by which religions can shape human behavior. Prestige psychology means that humans are predisposed to show deference toward individuals that display the key markers of prestige: generosity and benevolence, as well as being deferred to by other individuals. This applies to deities and supernatural agents, as well as flesh-and-blood individuals: a divine being that displays these traits can tap into human prestige psychology and prompt deference and imitation. As such, a deity or supernatural agent that not only displays prosocial tendencies, but also actively encourages the cultivation of prosocial dispositions among their followers can promote cooperation in a way that a punishing deity cannot. By promoting prosocial behaviors such deities/supernatural agents can enhance the fitness of the group of their followers, allowing their beliefs to spread through, for instance, cultural group selection. This process can be seen at work in the cultural dynamics of religions, including early and modern Christianity, which placed great emphasis on Jesus as a prestigious rather than dominant figure. Thus, religions need not be based on a vengeful, punishing God to promote group-beneficial behaviors. Instead there is an alternative pathway: benevolent, generous and prestigious gods can promote prosociality by tapping into our prestige psychology that is primed to defer to, and copy, such figures.

AUTHOR CONTRIBUTIONS

HL conceived the idea. HL and TM wrote the manuscript.

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From Physical Aggression to Verbal Behavior: Language Evolution and Self-Domestication Feedback Loop

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We propose that human self-domestication favored the emergence of a less aggressive phenotype in our species, more precisely phenotype prone to replace (reactive) physical aggression with verbal aggression. In turn, the (gradual) transition to verbal aggression and to more sophisticated forms of verbal behavior favored self-domestication, with the two processes engaged in a mutually reinforcing feedback loop, considering that verbal behavior entails not only less violence and better survival but also more opportunities to interact longer and socialize with more conspecifics, ultimately enabling the emergence of more complex forms of language. Whereas in the case of self-domestication, sexual selection has been proposed to work against physical aggression traits, in the case of verbal insult, the selection has been proposed to work in favor of verbal aggression. The tension between these two seemingly opposing forces gets resolved/alleviated by a tendency to replace physical aggression with verbal aggression and with verbal behavior more generally. This also helps solve the paradox of the Self-Domestication Hypothesis regarding aggression, more precisely why aggression in humans has been reduced only when it comes to reactive aggression, but not when it comes to proactive aggression, the latter exhibiting an increase in the advent of modern language. We postulate that this feedback loop was particularly important during the time period arguably between 200 and 50 kya, when humans were not fully modern, neither in terms of their skull/brain morphology and their behavior/culture nor in terms of their self-domestication. The novelty of our approach lies in (1) giving an active role to early forms of language in interacting with self-domestication processes; (2) providing specific linguistic details and functions of this early stage of grammar (including insult and humor); (3) supplying neurobiological, ontogenetic, and clinical evidence of a link between (reactive) aggression and (reactive) verbal behavior; (4) identifying proxies of the earlier stages in evolution among cognitive disorders; and (5) identifying specific points of contact and mutual reinforcement between these two processes (self-domestication and early language evolution), including reduction in physical aggression and stress/tension, as well as sexual selection.

Keywords: language evolution, self-domestication, reactive/proactive aggression, verbal aggression, neurolinguistics, language disorders, child development, sexual selection

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INTRODUCTION

Here we propose that human self-domestication (the presence in humans of morphological, physiological, behavioral, and cognitive features commonly found in domestic animals) co-evolved with a gradual transition from in-group (reactive) physical aggression to inter-group (complex) verbal behavior *via* (reactive) verbal aggression, in a mutually reinforcing fashion. We explore here in detail the possibility that the emergence of the simplest forms of language/grammar accelerated processes of self-domestication and brain evolution already underway, which in turn fueled the transition to more complex languages. Early verbal creations would have afforded an adaptive (non-violent) way to compete for status and sex (e.g., Progovac and Locke, 2009), accelerating/reinforcing self-domestication, while enhanced self-domestication provided a richer niche for extended communication and language learning enabling the transition to more complex forms of language.

Language – communication relying on syntax and grammar – is usually construed as a human-specific cognitive faculty that resulted from biological changes (e.g., Bolhuis et al., 2014; Chomsky, 2017). As a consequence, its history is generally reconstructed by looking for proxies of language in extinct hominin species and for (deep) homologs of language in extant species. By contrast, emergence and divergence of modern languages across the globe are presumed influenced by the physical environment, and social and cultural practices, with such influences largely confined to non-grammatical, lexical components. As a consequence, the history of languages is traced with a minimal reference to changes in brain, behavior, and cognition.

There is ample evidence that socio-cultural factors do indeed influence the divergence of modern languages, and this goes well beyond the attested effect of social factors on linguistic diversity within a language (as studied by Sociolinguistics) or on the lexicons of world languages (as studied by Anthropological Linguistics). For instance, the number of speakers seemingly contributes to explain the morphological complexity of languages (Lupyan and Dale, 2010). Likewise, computational modeling, experimental work with human learners, and language emergence in certain cultural contexts (like the *homesigns* developed by isolated deaf communities) have shown that core properties of language, such as duality of pattern or compositionality, can emerge by iterated learning and cultural transmission (Sandler et al., 2005; Tamariz and Kirby, 2016) and that the same cognitive and biological biases can result in different language features in different cultural environments (Thompson et al., 2016). Increasingly, however, evidence suggests that language structure also impacts on basic cognitive abilities, such as effects of word order on working memory (Amici et al., 2019). As a consequence, language features, language learning, and cognitive architecture comprise a reinforcing feedback loop (Deacon, 2003; Clarke and Heyes, 2017), wherein genetic changes occurred to accommodate language-specific cognition (Jablonka et al., 2012). The greater cognitive cost of language processing and learning incurred by certain recently evolved languages might have necessitated cognitive adaptation because of the enhanced demands on working memory and executive control (Benítez-Burraco and Kempe, 2018). In brief, we should expect not only that our cognitive architecture accounts for many aspects of the languages we speak, but also that certain language features, resulting from cultural and environmental factors, affect, more or less permanently, our cognitive architecture. These two aspects cannot be detached one from the other.

We have a good understanding of the morphological changes that apparently afforded language readiness, including brain rewiring associated with the globularization of the human skull/brain, which is a distinctive feature of our species when compared to the elongated shape found in Neanderthals and Denisovans (for details, see Boeckx and Benítez-Burraco, 2014a). Likewise, we also appreciate the changes in human behavior and culture that affect language structure and divergence[1]. However, we lack good hypotheses about the feedback loop between these two processes. One possibility is that the biological changes that brought about our species also favored the creation of the niche that enabled the emergence of aspects of language complexity *via* cultural evolution, which in turn affected our biology. Another possibility, not mutually exclusive, is that certain cultural practices affected our biology and paved the way toward specific cognitive changes that enabled the emergence of language complexity. Human self-domestication might have contributed to both processes, the evolution of our language-ready brain, mostly *via* biological mechanisms, and

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[1] These two processes are expected to have incurred in some sort of gradualism (which is not incompatible with occasional punctual sudden changes). In truth, gradual changes have been reported for the globularity of the human skull. According to Neubauer et al.'s (2018) study of endocranial casts, hominin fossils from first anatomically modern humans did not exhibit this type of globularity, in clear contrast to human skulls from more recent periods, which they found to be within the range of modern humans. They also identified an intermediate stage in the evolution of globularity, with the fossils dating somewhere between 130 and 100 kya. Overall, in the first step of this process, approximately 200–130 kya, the frontal area became taller, and the parietal areas and the cerebellum bulged and became larger, while the occipital area became more rounded. The second step, roughly 130–100 kya, involved size changes primarily in the cerebellar and occipital areas. Both steps contributed to the globular shape of the human skull. Neubauer et al. (2018) further suggested that the initial changes in the shape of the skull were caused by brain reorganization, rather than changes in the shape of the face, which are typically found in domesticated animals. Moreover, these morphological changes in the evolution of humans were not likely to have been a result of genetic drift, but rather of selection, given that there is evidence for positive selection of several genes expressed in brain development, including the genes responsible for axon and dendrite growth. Something similar occurs with our behavior, including our cultural practices. Based mostly on archeological findings, Mellars (2002) and others initially proposed that there was a major cultural and cognitive transition/revolution around 43–35 kya. However, later discoveries led to a revision of this view, pointing to a more protracted, gradual accretion of culture (see e.g., McBrearty and Brooks, 2000; McBrearty, 2007; Mellars, 2007, p. 3). Neubauer et al. (2018) further note that the globularization timeline parallels the emergence of behavioral modernity, culminating around 50–40 kya, suggesting that some of those genes expressed in brain development were selected and fixed. In summary, comparable to the morphology of the skull/brain, behavioral modernity also represents a culmination of gradual accretion over time, rather than a single rapid evolutionary event.

the creation of modern languages mostly *via* cultural mechanisms. Prior proposals linking language evolution with self-domestication in humans (e.g., Thomas and Kirby, 2018) seem to assume a unidirectional causal relationship, whereby self-domestication contributed to the emergence of language readiness and of complex languages. Such proposals have not advanced explicit hypotheses regarding how some specific language expressions/structures would have contributed to self-domestication processes and thus to the biological aspects of human evolution. Here we explore such a possibility in detail.

THE LANGUAGE EVOLUTION/ SELF-DOMESTICATION FEEDBACK LOOP: A HYPOTHESIS

Compared to our primate relatives (perhaps with the exception of bonobos), and to species of extinct hominins, present-day humans exhibit reduced aggression (Herrmann et al., 2011). Morphological changes indicative of reduced aggression appear in the fossil record alongside an increase in cultural artifacts, from around 80,000 years ago (Hare et al., 2012). The human self-domestication hypothesis (Hare, 2017) proposes that these changes evolved when natural selection favored increased in-group prosociality over aggression in human evolution. Accordingly, as a by-product of this selection, present-day humans are thought to exhibit most of the physical, physiological, and behavioral traits commonly found in domesticated strains of animals compared to their wild conspecifics, including reduced cranial robusticity and brain size, neotenic features (mostly affecting the face), reduced sexual dimorphism, reduced aggression, increased playing behavior, enhanced socialization, and reduced responsiveness to stress as measured by cortisol levels (Shea, 1989; Leach, 2003; Somel et al., 2009; Zollikofer and Ponce de León, 2010; Herrmann et al., 2011; Plavcan, 2012; Márquez et al., 2014; Fukase et al., 2015; Stringer, 2016). This is seemingly due to the fact that selection against aggression inhibits the proliferation of the neural crest cells (NCCs), ultimately affecting the development of many body components (Wilkins et al., 2014, but see Sánchez-Villagra and van Schaik, 2019 for some cautionary notes). Less aggressive behavior resulting from our self-domestication might have specifically enhanced learning and teaching opportunities and our capacity for knowledge exchange and group collaboration, ultimately supporting an increase in language complexity *via* a cultural process (Benítez-Burraco and Kempe, 2018 and Thomas and Kirby, 2018).

However, this broad picture has to be properly qualified. In spite of the trend toward increased in-group tolerance and prosociality, demographic pressures during the last part of our history seemingly increased inter-group aggression (Choi and Bowles, 2007). As a consequence, although reactive physical aggression (that which arises from fear or anger) has declined over time, inter-group proactive aggression (which strategically aims to achieve specific outcomes) has increased (Wrangham, 2018). Our proposal, which gives the emergence of language an active role, helps explain this otherwise surprising discrepancy between in-group and inter-group violence, which cannot be explained solely by self-domestication[2]. Interestingly, while proactive aggression seems to be tied to complex language/cognition, derogatory language, like swearing, is typically reactive, reinforcing our idea that it serves well to replace reactive physical aggression, specifically, and that it represents an early stage in the evolution of language complexity under the self-domestication hypothesis[3].

While some reactive physical aggression persists, it has been largely replaced by reactive verbal aggression. Verbal rituals have persisted throughout recorded history (Locke and Bogin, 2006; Locke, 2009). Such duels with words, as opposed to fists, provide an adaptive way to discharge aggressive dispositions (Marsh, 1978) and to compete without risking physical harm (Locke, 2008). Although verbal duels may be a cathartic purging of aggressive impulses, their beauty, creativity, artistic value, and cultural specificity have also been observed by many (Darmesteter, 1934; Samarin, 1969; and Pagliai, 2009). While linguists tend to focus on the language function of conveying information (and have tended to "sanitize" the language they study, excluding swearing, Bergen, 2016, p. 3), there are other, expressive, esthetic, and profane aspects of language, which are just as relevant in the context of language evolution (Haiman, 2013). Both verbal aggression and creativity are directly relevant to our proposal, showing the multiple adaptive advantages of using linguistic aggression over physical fighting (see section "Emergence of Proto-Syntax and Verbal Aggression (Insult)" for further discussion).

Direct verbal confrontation often makes use of simple forms of language, as illustrated with, e.g., crude compounds consisting of just one verb and one noun [e.g., English *kill-joy*, *pick-pocket, scatter-brain*, *turn-coat, cry-baby*; Serbian *cepi-dlaka* "split-hair," *vrti-guz* "spin-butt" (fidget), *ispi-čutura* "drink-flask" (drunkard), *jebi-vetar* "screw-wind"

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[2] Some differences exist between primate and human inter-group aggression, considering that humans usually form peaceful relationships and alliances among groups (see Wrangham and Glowacki, 2012 for discussion). Socially coordinated violence (proactive aggression) potentially became possible only with the onset of symbolic thought and complex cognition because the same capacities for communication and sociality allow warfare and conflict resolution and avoidance (Kissel and Kim, 2019). In fact, features of self-domestication reached a peak at the end of Upper Paleolithic (Cieri et al., 2014), right before collaborative inter-group conflicts became widespread during the Neolithic, as shown by genetic evidence (Zeng et al., 2018).

[3] While it may be true, as pointed out by a reviewer, that derogatory language can be used playfully in an endearing way, this is of course also true of physical aggression, such as hitting. This does not undermine the view that the primary function of both of these phenomena is aggression. As the reviewer also points out, complex language can certainly be used for derogatory purposes, even when seemingly polished and polite. This does not pose a problem for our approach, which associates such complex, pragmatically refined capabilities with the later developments in human evolution, which brought about more complex forms of language, with more sophisticated pragmatic skills, and, arguably, also more sophisticated tools for planning and coordinating proactive aggression.

(charlatan)]. As such, very simple grammars can suffice for verbal aggression and insult. Significantly, these compounds, which afford a particularly creative strategy for coining names with derogatory reference, have been analyzed as approximations of the earliest stages of grammar, showing both crude syntax and primitive vocabulary (e.g., Progovac and Locke, 2009; Progovac, 2015, 2016). Our hypothesis is that looking at the (gradual) emergence of verbal means of aggression (approximated by this kind of compound) might help illuminate the initial steps of the language evolution/self-domestication feedback loop. These verbal items would have afforded an adaptive (non-violent) way to compete for status and sex, first by derogating existing rivals and placing prospective rivals on notice; and second by demonstrating verbal skills and quick wittedness, both directly relevant for sexual selection (Progovac and Locke, 2009, p. 346)[4]. As a consequence, they would have accelerated/reinforced the effects of self-domestication on human behavior and cognition, promoting the transition to more complex forms of language. These types of verbal forms promise to make just a bit narrower the otherwise enormous chasm separating, on the one hand, expressions of emotion/aggression in animals, and, on the other hand, refined human language, with embedded sentences, and thousands of words expressing various subtleties of meaning. Code (2005, and references therein) offers evidence that swearwords are neurally distinct from the other words, relying both on brain areas where compositional language is processed, and on brain areas which support laughing and crying. In that sense, swearwords straddle the boundary between (animal) calls, which share many properties with laughing and crying, on the one hand, and compositional language, on the other. This reinforces the view that swearwords, which also often feature in insults, are primarily reactive, as are laughter and crying. Given that domestication processes can be long and protracted and not guaranteed to succeed either[5], it is important that we can identify factors that can reinforce it. According to our view, one of these factors was the gradual emergence of language itself (see also Sánchez-Villagra and van Schaik, 2019 for the importance of considering additional, synergistic factors, including language, in the considerations of self-domestication).

For concreteness, we postulate that this feedback loop was particularly important during the time period roughly between 200 and 50 kya[6]. This is a long time period when humans were not fully modern, neither in terms of their skull/brain morphology (and presumably, their cognitive abilities) and their behavior/culture nor in terms of their self-domestication (see Hare, 2017). During this time period, we propose to correlate the advances in human self-domestication processes with the emergence of simple forms of language/syntax, which were particularly suitable for the expression of verbal aggression. The novelty of our approach lies in (1) giving an active role to early forms of language in interacting with self-domestication processes; (2) providing specific details and functions of this early stage of grammar (including insult and humor); (3) supplying neurobiological, ontogenetic, and clinical evidence of a link between (reactive) aggression and (reactive) verbal behavior; (4) identifying proxies of the earlier stages in evolution among cognitive disorders; and (5) identifying specific points of contact and mutual reinforcement between these two processes (self-domestication and early language evolution), including reduction in physical aggression and stress/tension, as well as sexual selection.

One benefit of our proposal is that it helps solve the paradox of the two aggression types, reactive and proactive, which is raised by the Self-Domestication Hypothesis (SDH), that is, why proactive aggression has increased with time in spite of our increased self-domestication. The problem finds a direct solution in correlating early self-domestication processes with the emergence of simple forms of early language/grammar, featuring reactive verbal aggression; on the other hand, proactive aggression seems to be enabled in the later stages of self-domestication, which correlates with more complex forms of language (see Benítez-Burraco and Kempe, 2018; Kissel and Kim, 2019). The following stages outline our proposal (see also **Figure 1**):

1. *The first stage*, occurring roughly in the period prior to 200 kya, sees self-domestication processes only start to emerge, with reactive physical aggression still relatively high.
2. *The second stage*, occurring roughly from 200 to 50 kya, sees increased self-domestication favoring the emergence of early language forms with proto-grammars especially suitable for swearing and insult (i.e., reactive language), which began to gradually replace reactive physical aggression, serving the same function. This early language was insufficiently sophisticated to support proactive aggression. During this stage, there is an accelerated feedback loop between self-domestication processes and the solidification of the early forms of language, both promoting a reduction in reactive physical aggression.
3. *The third stage*, 50–10 kya (the Upper Paleolithic), saw self-domestication reach its peak. More cooperation and socialization and less reactive aggression created a niche for more complex forms of language and cognition.

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[4] Sexual selection is also thought to be one important triggering factor of self-domestication features, with females selecting less aggressive males, as discussed in section "Aggression, Verbal Behavior, and Sexual Selection."

[5] Künzl et al. (2003) found that long-term breeding and rearing of wild guinea pigs in captivity did not result in significant changes in behavior and hormonal stress responses in comparison to domestic guinea pigs. They concluded that it takes much longer periods of time, as well as artificial selection by humans, to bring about characteristics of domestication in wild animals. Human self-domestication did not involve artificial selection by others, and as such is not expected to have been instantaneous. Similar processes of slow self-domestication have also been observed in bonobos (Hare et al., 2012).

[6] Pending further evidence, this timeline, especially the starting point, has to be considered approximate. As pointed out by a reviewer, researchers have proposed that some forms of language with grammar may have been in place as early as 500 kya, based on the skeletal and genetic evidence from Neanderthals (e.g., Dediu and Levinson, 2013; see also Johansson, 2005; Zilhão, 2011).

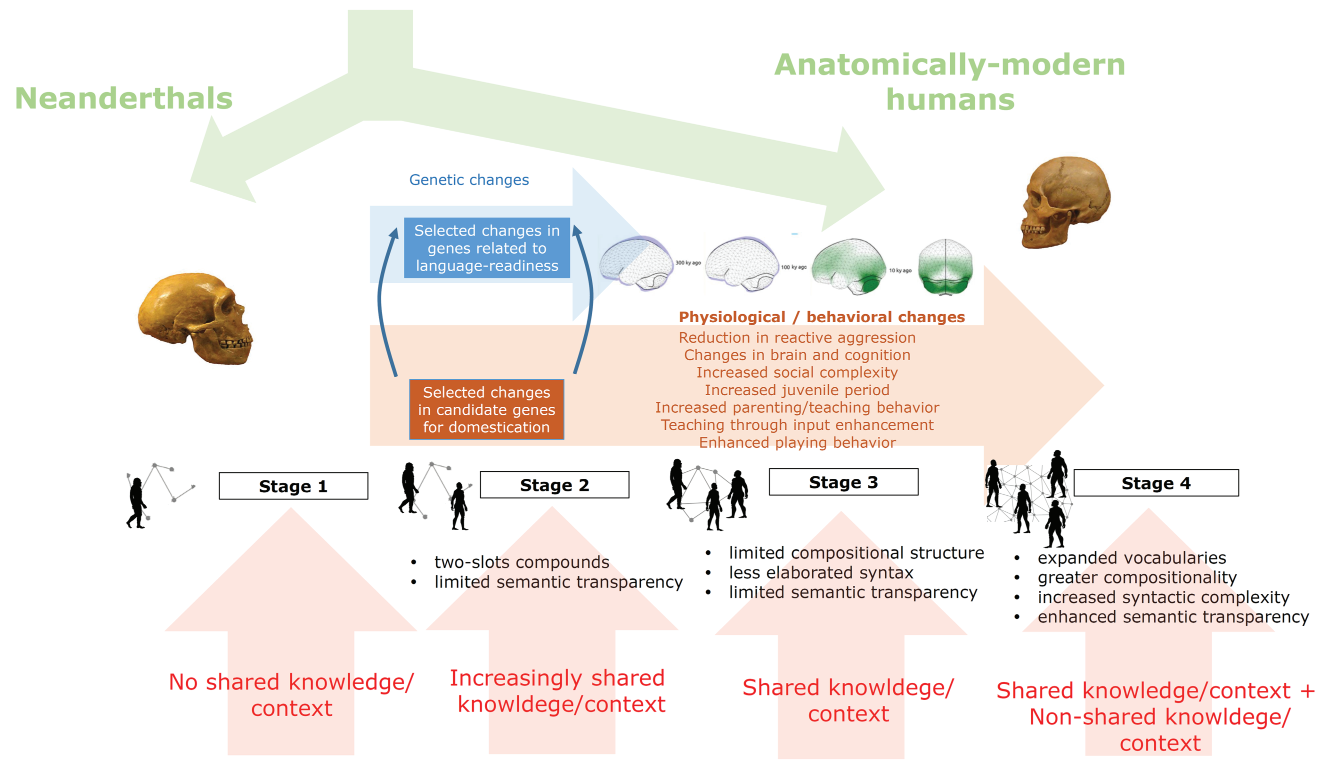

FIGURE 1 | A graphical summary of the hypothesis of how languages might have changed with time in our species under the effect of our self-domestication.

4. *The fourth stage*, from 10 kya (the onset of the Neolithic period) to the present day, was characterized by even more complex language and cognition, which now affords the linguistic, cognitive, and cultural means (e.g., sophisticated weapons) for coordinating premediated, large-scale, proactive aggression[7].

Our proposal regarding what characterized the second stage with respect to self-domestication and language evolution establishes a middle ground between two opposite but influential views, those of Chomsky and colleagues vs. Dediu and colleagues. On the one hand, based on their view of syntax/grammar as an undecomposable/unnegotiable block, Berwick and Chomsky (2011, 2016, also previous work) proposed that language/syntax emerged suddenly and recently, in its full complexity, "just a bit over 50,000 years ago" (Chomsky, 2005), with no possibility for any simpler stages or precursors, or "some 70,000–100,000 years ago, and does not seem to have undergone modification since then" (Bolhuis et al., 2014). On the other hand, based on the comparative evidence among *Homo heidelbergensis*' descendants, Dediu and Levinson (2013) proposed that language dates back to at least *H. heidelbergensis*, to some 500–400 kya, suggesting that Neanderthals and Denisovans might have even spoken complex languages comparable to those of modern humans, which would imply hierarchical and recursive syntax. We therefore acknowledge that our proposed timelines may be subject to revision pending further evidence. By contrast, in our proposal, this time period (roughly 200–50 kya) was characterized by a pre-hierarchical stage of languages, to contrast with the hierarchical and recursive stage, which is often associated with Chomsky's notion of Merge. To avoid potential terminological confusion, we will adopt the terms pre-hierarchical stage and hierarchical stage. While the pre-hierarchical stage is associated with rudimentary symmetrical, flat, and non-recursive grammars, the hierarchical stage is associated with the exact opposite: asymmetrical, hierarchical, (potentially) recursive syntax. Nonetheless, as will be discussed in the following section, there is continuity and common ground between the two types of grammar, with the pre-hierarchical stage directly foreshadowing the nature of the hierarchical stage itself.

Relevant to this debate is also the nature and significant degree of cross-linguistic variation attested in the expression

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[7] However, the picture is a bit more complicated. While there is a clear overall trend toward evolving self-domestication features in humans, including less masculinized traits in men, Cieri et al. (2014) found that Neolithic humans exhibit more masculinized features compared to Upper Paleolithic humans, as well as compared to present-day hunter-gatherers, attributing the effect to the more hierarchical and man-dominated nature of agricultural societies, where women have less opportunity to exert their sexual selection preferences, as compared to relatively egalitarian hunter-gatherer societies (see section "Aggression, Verbal Behavior, and Sexual Selection" for further discussion of these issues within a sexual selection scenario). It is also possible that proactive aggression contributed to this development, as it brings about wars, creating a new environment where stronger, more aggressive males would have been favored by both natural and sexual selection.

of the hierarchical stage (e.g., transitivity and tense) among extant human languages. Considering this variation in detail led to the proposal that these widely diverging hierarchical solutions were a later add-on, superimposed upon the common proto-syntactic foundation, and that the hierarchical layers of language may not have emerged only once and uniformly (in Africa) along with our species, but instead multiple times, and independently, either within Africa, or after the dispersion from Africa, plausibly in response to cultural pressures and innovations (Progovac, 2015, 2016)[8]. At least under the uniregional view of human origins, this would argue against hierarchical syntax emerging earlier than around 100–50 kya with humans[9].

EMERGENCE OF PROTO-SYNTAX AND VERBAL AGGRESSION (INSULT)

The use of profanity is characterized as "reactive language" (Bergen, 2016, p. 88) in the sense that it is typically impulsive and spontaneous, often referred to as automatic speech, or automatisms in aphasic studies (e.g., Jackson, 1884; Code, 2011). It contrasts with "intentional" language, which gets impaired in Broca's and global aphasias and which is more complex, demanding greater working memory. We contend that reactive language (e.g., swearing) is continuous with reactive physical aggression, having gradually replaced the latter, during the second stage (roughly from 200 to 50 kya).

Consider the following verb-noun compounds (1–3) from English, Serbian, and Twi, collected from various sources, old and new (English and Serbian examples are from Progovac, 2015; Twi examples are from Kingsley Okai, p.c., 2011)[10]. This type of compound is found across a variety of related and unrelated languages, with similar imagery across cultures (for specific examples and further references, see Progovac, 2015)[11]. It is of note that compounds like these have transient lives – they get created, and then the vast majority of them get abandoned, with only few surviving. As a result, different generations of speakers will be familiar with different compounds on these lists, taken directly from Progovac (2016, p. 8; further data can be found in Progovac and Locke, 2009 and Progovac, 2015). The significance of these compounds is also that they specialize for insult when referring to humans, in a variety of languages, reinforcing our view that simplest grammars are especially suitable for insult. There is no other grammatical strategy that we are aware of that specializes for insult, and certainly not a strategy with so many tokens.

1. kill-joy, turn-skin (traitor), hunch-back, wag-tail, tattle-tale, scatter-brain, cut-throat, cry-baby, fill-belly (glutton), crake-bone (crack-bone), fuck-ass, fuck-head
2. cepi-dlaka "split-hair" (hair-splitter); guli-koža "peel-skin" (who rips you off); vrti-guz "spin-butt" (restless person, fidget); muti-voda "muddy-water" (trouble-maker); jebi-vetar "fuck-wind" (charlatan); vuci-guz "drag-butt" (slow-moving person); kosi-noga "skew-leg" (person who limps); podvi-rep "fold-tail" (one who is crestfallen); liz-guz "lick-butt"; poj-kurić "sing-dick" (womanizer)
3. Atoto-botom "dip-pocket" (pickpocket); kukru-bin "roll-dung" (beetle); nom-mmogya "suck-blood" (vampire); wodi-nii "kill-person" (killer)

These creations specialize for derogatory reference and can be quite obscene and cruel. They are also humorous and creative, especially considering the simplicity of their structure. These compounds are coined by one single (non-recursive) operation merging just one verb and one noun (for illustration, see below; for further evidence and a discussion of alternative views, and possible variation across languages, see Progovac, 2015, 2019). Predominating among them are concrete, basic nouns, and verbs, depicting body parts and functions[12]. However, this rudimentary compounding strategy can produce stunning new concepts, often abstract. Their high imageability and coarseness contribute to the strong visceral effect. As metaphors, they demonstrate the cognitive innovations important for language, in particular, our ability to transcend the signature limits of core knowledge systems

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[8] According to, e.g., Stringer (2007) and Finlayson (2009), there are still many uncertainties about human timeline and dispersals. Stringer (2007, p. 17) mentions a possibility for an African version of multiregionalism, citing "growing molecular evidence of deep divisions within African populations" (see also Wong, 2017 for some recent findings). Under this scenario, hierarchical syntax could have emerged much earlier, independently among different populations in Africa, more in line with Dediu and Levinson's (2013) view.

[9] It is of note that Chomsky (2005) has also advocated a rather late emergence of hierarchical syntax, around 50 kya, as pointed out in the text. The difference is that on his approach syntax emerged suddenly in all its complexity, and uniformly, without any precursors, while on our approach syntax evolved gradually, and often differently in different populations, with precursors that interacted with the domestication and other processes involving the evolution of the brain. Also, for Chomsky, the evolution of syntax was fully biological/genetic, while in our view, it involves a complex feedback loop between culture and genes.

[10] Weekley (1916) collected a sizeable number of English verb-noun compounds. According to him, this expressive way of naming, often exhibiting unquotable coarseness, flourished in thirteenth and fourteenth centuries, yielding thousands of tokens. Mihajlović (1992) collected over 500 Serbian people and place names in this form, reporting that these condensed compositions pack in them "frozen fairy tales, proverbs, and ancient wisdoms and metaphors" (Mihajlović 1992, p. 8,9). Darmesteter (1934, p. 443) was impressed by the "artistic beauty and richness" of such derogatory compounds in French.

[11] Contrary to Nóbrega and Miyagawa (2015)'s view, in order for such compounds to count as approximations ("fossils") of early stages of syntax, they do not necessarily need to be found in every human language, with exactly the same characteristics (Progovac, 2019 offers a detailed defense of syntactic "fossils" in this sense). The claim is that this is the starting point, the bedrock upon which one can build (or not) various types of syntactic complexity, as discussed below. Different languages in fact offer different types of fossil structures in this sense, some of them rare to find across modern languages (as discussed by Progovac, 2015).

[12] See also Samarin (1969) for Gbeya insults, which also fixate on body parts and physical appearance. In fact, Mohr (2013) provides evidence that such vulgar expressions were completely appropriate to use in, e.g., Roman times, only 2 kya, clearly at the stage of advanced modernity. As she argues, the appropriateness of such language coincided with a much less strict sense of privacy in performing bodily functions, as well as in covering body parts with clothing. Whatever we might think of such language today, it played a much bigger role in ancient times.

and ultimately, to combine and unify conceptual units that belong to distinct domains (see Boeckx and Benítez-Burraco, 2014a for discussion). This enables us to metaphorize and metonymize, as well as to grammaticalize, and ultimately, to make languages change (see Benítez-Burraco, 2017 for discussion). They are thus also directly relevant for the consideration of cross-modality in the evolution of language, as discussed by, e.g., Cuskley and Kirby (2013) and Miyagawa et al. (2018).

These compounds exhibit features consistent with the primitive stages of language: grammatical simplicity; basic, concrete vocabulary; strong visceral effect; significant creativity; ability to transcend modalities to create new, abstract concepts (metaphoricity); ability to entertain and amuse (including humor); and continuity with complex syntax (see below). While these creations cannot be completely identical to what was created early in evolution[13], they can serve as excellent proxies, or approximations, which can be used to test current hypotheses, as well as to formulate new ones. Moreover, even though they certainly fall short of modern syntactic riches, they provide the foundation, the template from which to build modern syntaxes, as discussed below. As argued by, e.g., Gil (2005), such simple (associational) grammars are sufficient for many practical purposes.

While it is hard not to be distracted (or disturbed) by their extraordinary content, it is necessary to focus on the grammatical properties of these compounds. It is because of the most rudimentary nature of their grammar that these compounds qualify as approximations/proxies of proto-syntax. One concrete consequence of this type of two-slot grammar (which can only fit one verb and one noun, e.g., *turn-skin*) is that it cannot depict transitive events, which would require (at least) three slots (e.g., **snake-turn-skin*; or **snake-shed-skin*). In fact, this type of grammar is incapable of distinguishing subjects from objects (for further evidence, see Progovac, 2015). The noun in these compounds can be either subject-like (*cry-baby; rattle-snake; turn-table; tumble-weed*) or object-like (*turn-coat/skin; tumble-dung* (beetle); *fold-tail; split-hair*), and sometimes, it is hard to tell (e.g., *scatter-brain; busy-body; dare-devil*). Moreover, unlike their hierarchical counterparts in (4), verb-noun compounds in English (or Serbian) are not recursive (5), in the sense that the output of one binary operation of V + N (creating another N, *pick-pocket*) cannot serve as input to another binary operation, combining, e.g., the verb (V) *chase* with the noun (N) *pick-pocket*.

4. truck-driver chaser (the one who chases those who drive trucks)
5. *chase-pick-pocket (the one who chases those who pick pockets)

This simple binary stage of language directly foreshadows the nature of modern grammars in two important respects. First, modern grammars (with their so-called Merge operation) are considered to be binary, too, creating structures in a pair-wise fashion. Second, modern grammars rely heavily on nouns and verbs to express predications, i.e., who (noun) does what (verb). One can certainly imagine different kinds of grammars (ternary, n-ary), and different vocabularies depicting totally different concepts and relations, but modern human grammars are designed in a painstakingly binary fashion, and mostly for the purposes of expressing who does what (to whom). Such noun-verb combinations are at the bottom and the beginning of almost every modern sentence[14]. In fact, syntactic theory (e.g., Minimalism and predecessors) considers that every sentence unfolds from this bottom layer, which typically features a merge of just one verb and one noun (phrase), resulting in a Verb Phrase (VP) or Small Clause (SC), as given in (6). This analysis of the modern sentence is one of the most insightful and stable postulates in this theoretical framework. It was originally outlined by Burzio (1981), Stowell (1981), and Kitagawa (1985) and further solidified in the work of Koopman and Sportiche (1991), Chomsky (1995), Adger (2003), Citko (2011), and many others. This merge operation at the bottom of the hierarchy is sometimes referred to as First Merge in syntactic literature (e.g., Adger, 2003), whereas Second Merge adds a second argument (subject), in another, higher layer/segment of the verb phrase, which may be referred to as little vP (where TP is the Tense Phrase, responsible for the expression of tense and finiteness):

6. TP > vP > SC/VP[15]

If one intends to express both a subject and an object, together with the verb (7), one cannot do so with just a single binary operation (note that human grammars do not seem to allow ternary merges, but only binary ones; e.g., Kayne, 1984). This now requires first assembling an intransitive verb phrase or VP (a verb and one noun) (8a), and then taking that VP as an assembled unit and merging it with another layer of structure, little vP (8b). And the same is true for expressing tense/time – yet another layer, TP, is added for that purpose (8c). But, importantly, at the bottom of both transitive (7,8) and intransitive (9,10) sentences lies the binary, and possibly flat, small clause combination of just one verb and one noun (phrase)[16].

7. Petra will rattle snakes.
8. a. $[_{SC/VP}$ rattle snakes$]$ →
   b. $[_{vP}$ Petra $[_{SC/VP}$ rattle snakes$]]$ →
   c. $[_{TP}$ Petra will $[_{vP}$ ~~Petra~~ $[_{SC/VP}$ rattle snakes$]]]$

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[13] For example, while in modern languages, the categories of verbs and nouns are typically distinguished grammatically, this would not have been the case at the time when grammar/language just started emerging.

[14] It is also of note that Heine and Kuteva (2007) reconstructed a stage of human language evolution in which only nouns were used, followed by a stage in which both nouns and verbs were used, but no other categories, arguing that other categories gradually gammaticalize from nouns and verbs.

[15] The representation in (6) depicts the basic (partial) hierarchy of sentential structure, widely adopted in this syntactic framework. These are the least controversial layers, sufficient for our purposes, but there are certainly several others that have been postulated (see, e.g., Adger, 2003).

[16] It is of note that in some cases what counts as subject vs. object can get blurred, depending not so much on the noun's inherent relationship with the verb, but more on whether or not there are additional noun arguments. This is the case with the noun *snake* in the two derivations in the text. This is relevant for the claim that this bottom layer by itself is not capable of distinguishing subjects from objects. The reader should also note that these derivations are simplified by omitting certain steps and null categories (such as null v head), which are not relevant for the discussion.

9. Snakes will rattle./Petra will rattle.
10. a. [$_{\text{SC/VP}}$ rattle snakes] → [$_{\text{SC/VP}}$ rattle Petra] →
    b. [$_{\text{TP}}$ Snakes will [$_{\text{SC/VP}}$ rattle ~~snakes~~]] [$_{\text{TP}}$ Petra will [$_{\text{SC/VP}}$ rattle ~~Petra~~]]

The cross-out notation indicates the initial, underlying position of the subject in the small clause, before it moves to the TP layer. The Move operation in modern syntax can be seen as a strategy for connecting various layers of structure and, in this case, transforming the ancestral small clause into a full-fledged modern sentence. This certainly looks like a tortured, roundabout way to simply express who does what to whom. But this step-by-step building of modern syntactic layers, including transitivity, makes perfect sense if the original proto-grammar was preserved as the foundation upon which to build further layers, rather than discarded. It would have been a solid, sturdy step from which to reach for ever higher but shakier steps. The less plausible alternative would have been to step down first, to the platform with no grammar at all, and then start from scratch, trying to jump straight to the higher realms. But this would have resulted in very different modern grammars[17]. It is this binary requirement on building syntactic structure, already foreshadowed in the proto-grammar stage, that forces the hierarchy/asymmetry, which characterizes modern languages.

Even though our focus here is on verbal aggression and insult, the benefits of this kind of proto-grammar would have been much broader. This type of proto-grammar would have also provided a convenient strategy for naming animals [*tumble-dung; swish-tail* (*bird*)*; stink-bug*], plants (*tumble-weed; catch-fly*), objects, and places, as well as for expressing basic commands (e.g., *Catch fly! Turn snake!*) and statements (e.g., *Bug stink; Monkey see*), not to mention enhanced ways of thinking, because it enables one to create new concepts by merging two pre-existing concepts. They could have also been used for affective purposes between partners or for calming and comforting one's children (e.g., *Baby sleep*), also contributing to alleviating stress and tensions. In addition, according to Progovac (2015, 2016), an important extension of this two-*word* proto-grammar would have been two-*clause* symmetric combinations involving binary formulae (typically AB AC), often expressing wisdoms and observations (e.g., *You seek, you find; You sow, you reap; Easy come, easy go; Come one, come all; First come, first serve(d); Like father, like son; Monkey see, monkey do*)[18]. Such symmetric/paratactic clause combinations, where clauses stand next to each other, would have foreshadowed modern-day subordination/hypotaxis, where clauses get embedded one within another (e.g., *Those who seek will find*.).

In summary, the postulated approximations of proto-grammar provide continuity with modern syntax in two essential ways: (1) in their binary nature and (2) in their reliance on noun-like and verb-like elements to express predication. Even though it has become customary to reduce syntax to Chomsky's Merge, it is important to emphasize here that the combinatorics of syntax is just one aspect of it, determining how many elements can merge at a time (binarity), and how many times (recursion), and in which manner (flat or hierarchical). Human syntax/language is also undoubtedly designed to express predication, i.e., to express who does what (to whom), by using primarily verbs and nouns. Importantly, the way syntax became complex is not in just any old random way, but in a way that helps express, with more precision, who does what to whom (and when, and where, and how, and why)[19]. In both of these respects (binary combinatorics, and the focus on who does what to whom), verb-noun compounds are an excellent stepping stone into modern syntax. Importantly for our purposes, the proto-grammar strategy behind these compounds not only provides continuity with complex syntax but also provides a more graceful transition from animal cognition, and particularly, from animal behavior, i.e., their emotional vocalizations, to human behavior, *via* verbal aggression.

NEUROBIOLOGY OF PHYSICAL AGGRESSION AND REACTIVE LANGUAGE

The limbic system (a group of brain structures supporting emotion, motivation, and long-term memory; see Rolls, 2015 for review), the striatal regions, and parts of the cortex, particularly, the frontal and the temporal cortices (Dolan et al., 2002; Yang et al., 2009; Boccardi et al., 2011) support aggressive behavior. Highly aggressive subjects exhibit enlargement and atypical activation of striatal regions (particularly, the caudate; Gatzke-Kopp et al., 2009; Ducharme et al., 2012; Yang et al., 2017). The striatum has been associated with the dopamine system that governs the regulation of motivated behavior (Mogenson et al., 1980), and which is critically involved in the expression of aggression in animals (Rodriguiz et al., 2004), but it is also crucially involved in language processing (e.g., Krishnan et al., 2016; Viñas-Guasch and Wu, 2017). Domesticated rats exhibit size reductions of the striatal area (Kruska and Schott, 1977), and the limbic system exhibits the highest differences between domesticated animals and their wild conspecifics (reviewed by Kruska, 1988).

Similar brain areas are involved in both reactive and proactive aggression; however, only the latter is associated with a thinner anterior cingulate cortex (Yang et al., 2017), a region involved

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[17] One possibility would be n-ary (as opposed to binary) grammars, with certain designated slots with fixed ordering for tense, subject, verb, object, without grouping these categories into constituents and subconstituents, and without some of these categories exhibiting syntactic dominance over the others. One can also imagine languages that are not obsessed with who does what to whom. There seems to be nothing inevitable about evolving grammars with binary branching based on predication typically expressed by verbs and nouns.

[18] Such expressions are preserved much better in some languages than others (see Progovac, 2015, 2016 for discussion and references.) For a more theoretical discussion of the relevance of symmetry vs. asymmetry in human language and evolution, see also Citko (2011) and Progovac (2015).

[19] This is in fact where languages differ profoundly. There are several different strategies for discriminating between subjects/agents from objects/patients, including, but not limited to, ergative-absolutive grammars, split-ergative grammars, nominative-accusative grammars, serial verb grammars, and active-stative grammars. These strategies are distinct enough to pose serious challenges for linguistic analysis and description. In this approach, the emergence of transitivity is seen as a later evolutionary development, discovering different solutions to the same problem posed by the limitations of the most rudimentary of grammars.

in the regulation of emotions and social behavior including conflict monitoring and empathy (Devinsky et al., 1995; Botvinick, 2007). The cingulate gyrus, which is part of cingulate cortex, plays a key role in language processing, contributing to speech production *via* its connections with Broca's area (Bernal et al., 2015). Compared to chimpanzees, bonobos (who are less aggressive) exhibit stronger links between the anterior cingulate gyrus and the amygdala, a pathway involved in the inhibition of aggression (Rilling et al., 2012). Likewise, Roth and Strüber (2009) found that reactive aggression is associated with smaller, less active frontal brain structures and amygdala hyperactivity, whereas proactive aggression correlates with reduced response of the amygdala and of cortical regions related to empathic and social behavior. Compared to chimps, bonobos also show an enlarged dorsal amygdala (Rilling et al., 2012). The amygdala is also implicated in the activation of the hypothalamic-pituitary-adrenal (HPA) axis through connections with the hypothalamus (Davis, 1997; Ledoux, 1998). The HPA axis is a major neuroendocrine system encompassing the hypothalamus, the pituitary gland, and the adrenal glands and regulating a great number of bodily functions. A reduced response of the HPA axis to stress has been observed in most domesticated animals (Kruska, 1988; Künzl and Sachser, 1999; Trut et al., 2009). With respect to aggression and cognitive functioning, reactive aggression in humans is associated with lower levels of goal-oriented inhibition and higher levels of flexibility, and proactive aggression is associated with higher levels of working memory (Hecht and Latzman, 2018)[20].

In comparison to other forms of language, the processing of swear words/profanity entails more involvement of the basal ganglia, limbic structures, thalamus, and the right hemisphere (e.g., Code, 2005, 2011; Bergen, 2016). The basal ganglia (i.e., the striatal regions) and the limbic system are also highly implicated in physical aggression. Disorders, which result in uncontrolled swearing/profanity, typically involve a basal-limbic connection dysfunction (discussed further in section "Disorders"). Basal-limbic structures are phylogenetically old, and the aspects of human communication associated with them are considered to be ancient, too (Van Lancker and Cummings, 1999; Bradshaw, 2001; Bergen, 2016), a potentially controversial claim (although see also Lieberman, 2000, 2009 on the ancient nature of basal ganglia). In this respect, Code (2005, p. 317) suggests that these forms of language might represent fossilized clues to the evolutionary origins of human communication. With brain damage affecting inhibitory processes, primitive behaviors (e.g., verbal automatisms) can emerge from primitive regions. In fact, damage to language centers in the brain can obliterate most language but leave swearing and expletives intact (see section "Disorders" for more details).

Differential impairment of reactive language versus intentional language implies that they employ distinct neural bases/pathways (Bergen, 2016, p. 87). The circuit that supports reactive language (including profanity) is evolutionarily far older, dominated by the limbic system, responsible for generating emotions and motor impulses, where the basal ganglia regulates and selectively suppresses such impulses (Bergen, 2016, p. 95). In disorders, such as Tourette's syndrome with coprolalia, there is a failure of this regulatory function of basal ganglia (see section "Disorders"). The relevance of basal ganglia for emotional speech processes, including such basic emotions as fear and disgust, is also established in the work of Paulmann et al. (2009) and Péron et al. (2013). Emotional vocalizations by other primates and mammals also seem to be supported by this kind of pathway, involving the limbic system and the basal ganglia (Robinson, 1967; see also Gruber and Grandjean, 2017), suggesting that emotional, profane language has some continuity with emotional vocalizations in other animals.

In natural use, expletives, especially those that are highly taboo, elicit strong physiological responses (including increased heart rate and sweating; Bergen, 2016). Such words are used for fundamental expression of deep emotion, including fear, pain, frustration, as well as for sex and violence (Code, 2005). The use of profanity is more common in men than in women (Jay, 1980, 1995; Van Lancker and Cummings, 1999, but see section "Aggression, Verbal Behavior, and Sexual Selection" for a possible challenge to this view), and this is true even in language disorders (Code, 1982, 2011; Jankovic and Rohaidy, 1987; Bergen, 2016). Considering that reactive physical aggression is more frequent in men than in women and that self-domestication was primarily subject to sexual selection (see section "Child Development"), this parallelism between physical and verbal aggression reinforces our hypothesis that verbal aggression acts as a proxy/replacement for reactive physical aggression.

Finally, expletive compounds can be highly humorous. One of the main functions of humor is to provide relief from stress and tension, *via* laughter and mirth (Berlyne, 1972; Meyer, 2000; Buijzen and Valkenburg, 2004). Humor serves as a natural stress antagonist in situations of trauma and stress, by decreasing cortisol levels (Vrticka et al., 2013; Bains et al., 2014). Typically, wild animals exhibit a more pronounced cortisol response to stress, compared to their domestic counterparts (Künzl and Sachser, 1999; Künzl et al., 2003; Zipser et al., 2014; Kaiser et al., 2015). As noted above, domestication is associated with a reduction in the function of the HPA axis (Naumenko and Belyaev, 1980; Kruska, 1988; Oskina, 1996; Künzl and Sachser, 1999; Trut et al., 2009). Humor engages a core network of cortical and subcortical structures, including the meso-cortico-limbic dopaminergic system and the amygdala (Vrticka et al., 2013). In addition, humor can often serve as a form of strong assertiveness bordering on aggression, especially in cases of teasing and insult (see section "Child Development"). We therefore argue that humor's dual functions (i.e., stress reduction function and verbal aggression), and its reliance on limbic structures supports our proposition that early forms of language provided relief from stress and tension, as well as a (verbal) alternative to reactive aggression, and thus reinforced the effects of self-domestication.

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[20] In this respect, Wynn and Coolidge (2004) proposed that working memory may have been enhanced in modern humans, compared to Neanderthals, contributing to the capacity for innovation and experimentation. It is also pointed out by Balari et al. (2013) that enhanced working memory may have enabled recursive syntax. Finally, Benítez-Burraco and Kempe (2018) linked the enhancement of working memory to the emergence of languages with expanded vocabularies and more complex syntax, which are purportedly optimized for conveying complex meanings and know-hows to people not sharing a common ground or a common cultural knowledge.

DISORDERS

Of particular relevance to our hypothesis are disorders that exhibit an imbalance between inhibition and disinhibition of verbal aggression. In this section, we consider certain disorders, which imply a dissociation between derogatory language and (more complex) referential language. Some of these conditions have a genetic basis, with candidate genes positively selected in our species.

Tourette's Syndrome and Coprophenomena

Tourette's syndrome (TS) is a hereditary tic disorder affecting the basal ganglia and the basolateral amygdala and hippocampal formation, circuitry involved in social decision making (Albin, 2018). It is sometimes accompanied by involuntary obscene speech and derogatory comments (coprolalia). Less commonly, TS patients may also exhibit copropraxia, which involves involuntarily making obscene gestures (Jankovic and Rohaidy, 1987; Singer, 1997; Freeman et al., 2009; Bergen, 2016). Although these coprophenomena and the TS syndrome more generally remain poorly understood, brain imaging, neurophysiological, and post-mortem findings implicate the cortical-striatal-thalamocortical pathways in the etiopathology of TS (e.g., Mink, 2003; Singer, 2005; Singer and Minzer, 2005; Ganos et al., 2013). These pathways overlap with striatal-cortical networks implicated in physical aggression (as discussed above) and with the Broca's-basal ganglia network essential for speech and language processing (e.g., Lieberman, 2000, 2009, 2015; Ullman, 2006). TS also tends to include repetitive involuntary eye, facial, and head movements, as well as explosive outbursts (Budman et al., 2008; Kano et al., 2008; Chen et al., 2013; Ganos et al., 2014). Given that the major functional role of eye, face, and head movements is social signaling, Albin (2018) suggested that the coprophenomena associated with TS may be best understood as distortions of reactive, spontaneous social signals, thus possibly implicating the brain areas involved in TS in the evolution of early language. The use of foul reactive language at the early stages of human self-domestication may have strengthened these brain circuits, easing the way into more complex forms of language[21].

Patients with TS experience an increase in their tics under stressful conditions, which are accompanied by a sense of discomfort that is relieved by tic performance (e.g., Cohen and Leckman, 1992; Leckman and Peterson, 1993; Evers and van de Wetering, 1994; Jankovic, 1997; Banaschewski et al., 2003; Kwak et al., 2003; Woods et al., 2005; Corbett et al., 2008; Albin, 2018). Importantly, a subset of TS patients exhibits heightened reactivity to stress of the HPA axis (Chappell et al., 1994). Likewise, children with TS show higher cortisol levels in response to stressors, which are indicative of an enhanced HPA responsivity to stress (Corbett et al., 2008). This is relevant to the self-domestication hypothesis of human evolution, because, as noted above, domestication entails reduced response of the HPA axis to stress. In this respect, TS can be seen as exhibiting attenuated features of self-domestication, positing an intriguing parallelism with autism, also proposed to exhibit some features of a less-domesticated phenotype (Benítez-Burraco et al., 2016).

Rare mutations in selected genes have been identified in some TS patients. One of these genes is *SLITRK1*, which encodes an integral membrane protein involved in neurite outgrowth (Miranda et al., 2009). *SLITRK1* has an evolutionarily conserved expression pattern in projection neurons of the corticostriatal-thalamocortical circuits and cortical pyramidal neurons, contributing to the development of connections between the cortex, the striatum, and the thalamus (Stillman et al., 2009). Incidentally, there is also an ancestral mutation of *SLITRK1* (S330A) that has been related to TS (Ozomaro et al., 2013; Alexander et al., 2016). This SNP is highlighted by Theofanopoulou et al. (2017b) as a sort of window to the "underdomesticated" phenotypes found in other hominins. Overall, these genetic findings suggest that TS is more related to ancestral genomic variants than to derived changes in modern humans.

Aphasia and Speech Automatisms

Aphasias, resulting from brain damage, involve disinhibition of speech automatisms, such as counting, rhyming, prayer, but most commonly expletives and modal/auxiliary sentence stem structures (e.g., *I cannot*; *I try*; Code, 2005, 2011; Code et al., 2009). These two most frequent subtypes are also most relevant for evolutionary considerations. For the severest cases of non-fluent aphasia, these automatisms may be the only speech produced (Code, 2011, p. 139). Speaking specifically about derogatory language, Code (2011) points out that naturally occurring expletives emerge from ancient areas of the limbic system (see also Code, 1987; Leckman et al., 1991; Speedie et al., 1993; Van Lancker and Cummings, 1999). On the other hand, in pathology, expletives seem to emerge from disinhibited basal-limbic structures, which are normally under control from prefrontal networks, where basal ganglia damage appears to be essential for the production of an aphasic automatism (Brunner et al., 1982). With aphasias, we witness a loss of the complex compositional language, while the reactive, derogatory language is preserved. According to the so-called last in, first out principle (see e.g., Code, 2005; also Gibson, 2009), what is acquired last is the most shallow/fragile layer

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[21] A reviewer points out that the mainstream view of the evolution of language has shifted away from biological evolution to cultural evolution. While it is true that trends in scientific research often bend in this and then that direction, especially with the questions having to do with nature vs. nurture, our proposal is that both biology and culture are directly involved and that the relevant challenge is to identify phenomena that can be shown to be so intertwined. Our paper presents an attempt in this direction, invoking a complex feedback loop between cultural innovations and biological selection. Importantly, our proposal is detailed enough to allow empirical testing. In this respect, we point out that genetic mutations affecting *FOXP2* and other genes increased synaptic plasticity and neuronal connectivity of the human brain (e.g., Hillert, 2014; Dediu, 2015), particularly in the frontal-striatal network, likely enabling human capacity for more complex language (see also Boeckx and Benítez-Burraco, 2014b). The finding that these networks have a biological foundation, supported by multiple genes, suggests that the emergence of complex syntax/language was not only a cultural invention but also a biological/genetic event.

that is the easiest to lose, and vice versa. In other words, the most recently evolved components of cognition, which certainly include compositional language, are the least robust, and most prone to damage and loss. If true, this provides further evidence of the role of reactive verbal aggression in language evolution.

This raises the question of whether the production of automatisms is associated with a higher degree of stress, and whether such production helps relieve stress. While there are many reports to the effect that aphasics in general experience a lot of stress and anxiety, even anger, specifically in trying to use language (see e.g., Goldstein, 1942; Luria, 1970; Laures-Gore et al., 2007; Cahana-Amitay et al., 2011; Laures-Gore, 2012), we have not come across any reports addressing specifically the production of automatisms in this respect. It would be of interest for future research to determine whether or not the incidence of specifically cursing and derogatory automatisms correlates with the experience of higher stress and anger (and thus higher cortisol levels), as well as whether the uttering of such automatisms helps relieve stress, in a way comparable to the production of tics in TS (section "Tourette's Syndrome and Coprophenomena").

In summary, our discussion of language/cognitive disorders in relation to self-domestication and language evolution supports the view that these disorders can inform on aspects of human domestication. They, moreover, involve patterns of inhibition and disinhibition that seem to be just poles on the continuum of cognitive modes, encompassing also the typically developing cognition. The discussion of disorders also highlights the existence of significant individual variability across all the dimensions relevant for language processing, which, moreover, seems to be genetically influenced. These considerations suggest that the evolution of language cannot be a simple, straightforward step, but rather a complex, multi-faceted, and multi-gene phenomenon, recruiting and coordinating a variety of cognitive systems and functions, with each new development potentially subject to genetic and/or cultural evolution.

CHILD DEVELOPMENT

While ontogeny does not literally recapitulate phylogeny, there are usually points of comparison (e.g., Ridley, 1993). Here we report on some notable parallels between childhood development and our model of language evolution, with a focus on aggression, verbal (derogatory) behavior, and complex language. First, in the transition from infancy to childhood, when syntax emerges, there are developments in three other relevant areas: the ability to spontaneously coin compounds (Becker, 1994); the tendency to tease and insult, and thus, the onset of humor (McGhee, 1976; Apte, 1985); and the onset of agonistic verbal engagement or verbal dueling (Gossen, 1976; Wyatt, 1995, 1999). Second, as noted by these and other authors, teasing and insulting, as well as verbal dueling, tend to predominate in males, even at the time of their appearance in late infancy or early childhood, pointing to the relevance of sexual selection, and providing further supporting evidence for our proposal.

Regarding the emergence of syntax, children use simpler/simplified syntactic structures early on, and combinations of just one verb and one noun (intransitive structures) predominate in early child grammars cross-linguistically. It is beyond the scope of this paper to get into different types of theories and controversies behind these omissions/simplifications, as the literature on this topic is vast and varied. Suffice it to note here that, at least on the surface, early children grammars often express only one noun argument per verb (see e.g., Zheng and Goldin-Meadow, 2002; Rakhlin and Progovac, 2017). Children's early utterances also include novel compounds of various kinds, including noun-noun and verb-noun combinations, for example, light-man (electrician); nose-beard (whiskers); and push-ball (a ball for pushing and bouncing; Becker, 1994). Compounding of this type seems to be a rather simple, straightforward strategy for children expressing new concepts.

There are also experiments targeting specifically compounds using verbs and nouns, establishing a clear difference in the order and ease of acquisition between flat verb-noun compounds and their hierarchical counterparts. In their experiment, Clark et al. (1986) prompted children to produce hierarchical *-er* compounds (e.g., *This is a cheese-grater*; *paper-ripper; ball-bouncer*). At around three, instead of these targeted compounds, children consistently produced related verb-noun combinations (i.e., *This is a grate-cheese; rip-paper; bounce-ball*). Before reaching the target adult-like stage, many children also experienced another stage, where they produced compounds with misplaced affixes (i.e., *This is dry-hair-er/dry-er-hair* in lieu of *hair-dry-er*) or (*This is a fix-bik-er/fix-er-bike* in lieu of *bike-fix-er*).

Some conclusions from child language studies are important for our hypothesis. First, the stages and struggles in the acquisition of these compounds reinforce the view that *-er* compounds are related to VN compounds, as both rely on the common foundation provided by the flat (paratactic) verb-noun composition. Second, children start with the simpler structures, with the foundation, before they can scaffold to the hierarchical supra-structure, as emphasized by Clark et al. (1986). Third, VN compositions seem to be more primary and simpler than their hierarchical relatives.

With regard to the second area of development, namely, the onset of humor (and the tendency to tease and insult), laughter is one of the first social vocalizations in human infants, with an early onset at approximately 4 months of age (Ruch and Ekman, 2001). Responsive smiling generally develops even earlier, within the first 5 weeks (Kraemer et al., 1999). The earliest form of humor in young children, incongruity-based humor, relies on principles of discrepancy applied to actions, such as clowning and acting silly (McGhee, 1976). This kind of humor has also been reported for other primates (Patterson and Gordon, 1993). McGhee also reports a gender difference emerging at the age of 6–11 years old, but not before that. Specifically, he found that boys laughed more frequently than girls (the girls instead tended to smile), that they initiated humor more often, whether by non-verbal or verbal means, and that they also showed more hostility in their laughter and humor, including ridicule and insult. McGhee concluded that attempts to initiate humor or laughter in the presence of others can be seen as a form of strong assertiveness, especially in the case of hostile humor. This is directly relevant for our hypothesis of verbal aggression (partly) replacing physical aggression, which also predominates in males.

Finally, concerning the third area of development that we wish to highlight (the onset of agonistic verbal engagement or verbal dueling), it has been found that, cross-culturally, boys aged 3–11 engage in rough and tumble play, as well as verbal aggression, significantly more than do girls (Whiting and Edwards, 1973; Apte, 1985, p. 71; but see Björkqvist, 2018, for a possibly different view). Likewise, in many cultures, adolescent boys and men tend to engage in ritual insults (e.g., Apte, 1985, p. 70). Marsh (1978) provides convincing evidence from a variety of situations and cultures that ritual insult exchanges often serve instead of physical violence. This is consistent with our view that verbal aggression provides a different channel to the same goal, involving less risk of physical harm, thus contributing to better survival.

AGGRESSION, VERBAL BEHAVIOR, AND SEXUAL SELECTION

Self-domestication in humans has been attributed to sexually selective forces, including selection against (physical) aggression, and in favor of pair-bonding beneficial for child rearing (Hare et al., 2012; Stanyon and Bigoni, 2014; Okanoya, 2015; Gleeson, 2018). Likewise, the emergence of early grammars, especially suited to verbal aggression (insult), has been attributed to sexual selection for creative cognitive abilities (Progovac and Locke, 2009; Progovac, 2015). Furthermore, the use of both verbal and physical aggression seems more prevalent in males, revealing a dimorphism characteristic of sexual selection. Starting early on in childhood, and continuing into adulthood, across a variety of cultures, both physical aggression and verbal aggression show significant gender differences in favor of males (Whiting and Edwards, 1973; Apte, 1985), including with language disorders (Code, 1982, 2011; Jankovic and Rohaidy, 1987; Bergen, 2016). This gender discrepancy in both types of aggression suggests that they cluster together and that they have a common underlying cause, consistent with our proposal that verbal aggression served to replace (reactive) physical aggression.

Franks and Rigby (2005) observed that men increase their creativity with language in the presence of both attractive women and male competitors. Creativity is highly correlated with intelligence (Miller, 2000), implicating creative language use in both mate attraction and intra-sexual competition in men. Furthermore, eloquent speakers tend to be granted the highest social status (Tallerman, 2013, p. 95), which in turn is correlated with greater reproductive success (Locke, 2009). Following Gleeson (2018, p. 8), we contend that any increase in language complexity may imply selection forces favoring such complexity (see Progovac, 2019), directly implicating sexual selection in the proliferation of more complex, creative language.

Furthermore, while sexual dimorphism has decreased in humans during the period of self-domestication, it has certainly not been eliminated. In his review article, Gleeson (2018) makes a case for the relevance of sexual selection in the evolution of humans, and he observes that female preferences must have been for moderately masculine males, rather than for extremely non-masculine (domesticated) ones, likely reflecting conflicting forces in sexual selection[22]. On the one hand, there are female preferences for male investment in pair-bonding, but on the other hand, there are also female preferences for physically stronger, more masculine males, which seem to be context-dependent, and to vary relative to environmental and other circumstances, related to survival (Trivers, 1972; Kruger, 2006; Archer, 2009; Quist et al., 2012). Boothroyd et al. (2017) found that moderately masculine fathers had more surviving offspring than those with both relatively low and relatively high masculinity, suggesting a centralized optimum of masculinity. It is also worth observing that some indicators of masculinity have infiltrated language, including low vocal pitch, as well as the initiation of humor, often analyzed as building and then resolving tension/incongruity, and considered by McGhee (1976) to reveal strong assertiveness, especially given that it involves a risk of failure. Both of these features seem to be subject to female preferences, possibly indirectly contributing to the preservation of (moderate) masculinity.

Furthermore, males exhibit displays of physical prowess to the formidability of male competitors, as well as characteristics such as facial hair and low vocal pitch, that increase perceptions of dominance (Hill et al., 2017). These traits are of direct relevance for sexual selection because they show sexual dimorphism, they emerge around puberty, and they correlate with success in mating and reproduction. Importantly, the specific derogatory compounds, which we argue are reflective of early language, are illustrative of both inter- and intra-sexual selection. Regarding male to male competition, these compounds often describe men in derogatory terms, but even when they seemingly describe women, such compounds are still typically used to derogate men, for a doubly insulting effect (Mihajlović, 1992; Progovac and Locke, 2009)[23]. As pointed out by Marsh (1978), the most frequent type of insult among men even today has to do with emasculating one's opponent. Their usefulness in derogating existing rivals and placing prospective rivals on notice (aggressive rivalry), and in demonstrating verbal skills, humor, and quick wittedness simultaneously engages both sides of the sexual selection equation (Progovac and Locke, 2009). Such verbal items would have afforded a particularly useful, low-risk (non-violent) way to compete for status and sex. Of direct relevance for our proposal is Hill et al.'s (2017) conclusion that intra-sexual selection led to enhanced same-sex

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[22] Gleeson and Kushnick (2018) provided evidence in favor of sexual selection *via* female preference for less aggressive males, leading to reduced sexual dimorphism, but only in the societies where females have relatively high social status, high enough to be able to choose. Furthermore, this effect is more robust where food resources are more secure. In the case of food scarcity, even when females can exert a choice, the tendency is toward selecting stronger (more aggressive) males.

[23] As discussed by Progovac and Locke (2009), even compositions that seem to describe females (*laj-kučka* "bark-bitch," loud, and obnoxious person; *plači-pička* "cry-cunt," vulgar version of *crybaby*) are in fact typically used in reference to males.

intimidation, or formidability, instead of actual combat. In this respect, derogatory language can be viewed as the most innovative and creative means of achieving such "formidability," which straddles the boundary between physical and cognitive strength.

According to Card et al.'s (2008) meta-analytic review of 148 studies, there exist clear gender discrepancies favoring boys in direct (reactive) aggression, and only trivial differences favoring girls in indirect aggression (see also Björkqvist, 2018). While Björkqvist (2018) suggests that boys and girls are equally aggressive when it comes to verbal aggression, the evidence for this claim is not provided in this opinion piece, and it contradicts many reports which have found such a difference favoring males in verbal aggression, whether with typical populations [section "Neurobiology of Physical Aggression and Reactive Language"], or impaired populations (section "Disorders"). While reactive physical aggression in humans has seen a decline, as discussed at length in the previous sections, it still exists, and it (still) shows a prominent gender difference. According to, e.g., Archer (2009), the extent and the nature of gender differences in aggression can be better explained by sexual selection, given that they increase with the degree of associated risk, occur early in life, and peak in young adulthood.

There are also gender differences in initiating and perceiving humor. Adolescent and adult females exhibit greater emotional reactivity during humor perception than do males (Vrticka et al., 2013). This supports the fitness indicator hypothesis of humor, related to female preferences. Unlike with humor appreciation, where striatal activation follows or coincides with activation of temporal regions, with humor creation (which exhibits a male bias), the peak striatal activation precedes the peak of temporal activation (Amir and Biederman, 2016). The striatum (basal ganglia) is also implicated in both physical and verbal aggression. Both types of gender differences, those associated with the initiation of humor, and those associated with the appreciation of humor, directly implicate sexual selection in the feedback loop that we propose was critical to the evolution of language and self-domestication.

Three hormones were likely targets for sexual selection with respect to a reduction in physically aggressive behavior: serotonin, testosterone, and oxytocin (Kuepper et al., 2010; Montoya et al., 2012). Low testosterone has been related to male prosociality and parental care (Burnham, 2007). Exogenous serotonin increases harm avoidance and cooperative behavior (Wood et al., 2006; Crockett et al., 2010) and increases in brain levels of serotonin correlate with reduced emotional reactivity and aggression in experimental animal populations selected for friendliness toward humans (Plyusnina et al., 1991; Agnvall et al., 2015). In domesticated animals and bonobos, an increase in serotonin and a reduction in testosterone are associated with facial feminization and reduced cranial capacity (Hare et al., 2012). Although archaic human species had similar sized brains compared to *H. sapiens*, their faces seem to be more masculinized than the oldest modern humans (Churchill, 2014; Hare, 2017). It is also relevant that changes in the brain seem to have predated changes in our face morphology, possibly because of our mild self-domestication at that initial stage. Finally, oxytocin has been claimed to modulate the multimodality that characterizes higher-order linguistic abilities, including the vocal-auditory system, the attentional-memory system, and the socio-interactive system (Theofanopoulou, 2016) because of its regulatory role on the development of specific neural pathways (e.g., Theofanopoulou et al., 2017a on vocal learning).

We thus conclude that sexual selection of self-domestication interacts with sexual selection for verbal aggression, possibly in conflicting ways, which may account for the complicated picture of the expressions of masculinity described above: while the former favored less physically aggressive males, the latter favored verbal behavior/aggression, which, at early stages of language emergence, brought about novelty, creativity, and verbal humor. The net result would converge on selecting those who are not just less aggressive, but who are also better able to use verbal aggression to replace physical aggression, as they would be selected by both processes. This contrasts with the conclusion reached by Stanyon and Bigoni (2014), who argue that it was reduced male competition and increased female choice that favored cognitive evolution. While this is certainly one part of the story, our proposal implies that the continued male competition in the realm of verbal aggression/verbal behavior also contributed substantially to the evolution of cognitive abilities, at least at this early but crucial step in the emergence of language and evolution of self-domestication.

DISCUSSION AND CONCLUSIONS

Here we proposed that that self-domestication favored the emergence of a phenotype prone to replace reactive physical aggression with verbal aggression. The (partial) transition to verbal aggression and verbal behavior more generally then favored self-domestication, *via* a mutually reinforcing feedback loop, since verbal behavior affords less violence, better survival, and more opportunities for social interactions, ultimately paving the way for the evolution of more complex forms of language. We further proposed that looking at the (gradual) emergence of verbal means of aggression (approximated by proto-grammatical compounds) helps illuminate the initial steps of the language evolution/self-domestication feedback loop. The novelty of our approach lies in (1) giving an active role to early forms of language in interacting with self-domestication processes; (2) providing specific details and functions of this early stage of grammar (including creative uses of insult and humor); (3) supplying neurobiological, ontogenetic, and clinical evidence of a link between (reactive) aggression and (reactive) verbal behavior; (4) identifying proxies of the earlier stages in evolution among cognitive disorders; and (5) identifying specific points of contact and mutual reinforcement between these two processes (self-domestication and early language evolution), including reduction in physical aggression and stress/tension, as well as sexual selection.

One immediate advantage of our proposal is that, as noted, it helps solve the paradox of the two aggression types, reactive and proactive, which the Self-Domestication Hypothesis (SDH) on its own cannot solve. If SDH simply postulates that humans were selected for their friendliness and lack of aggression,

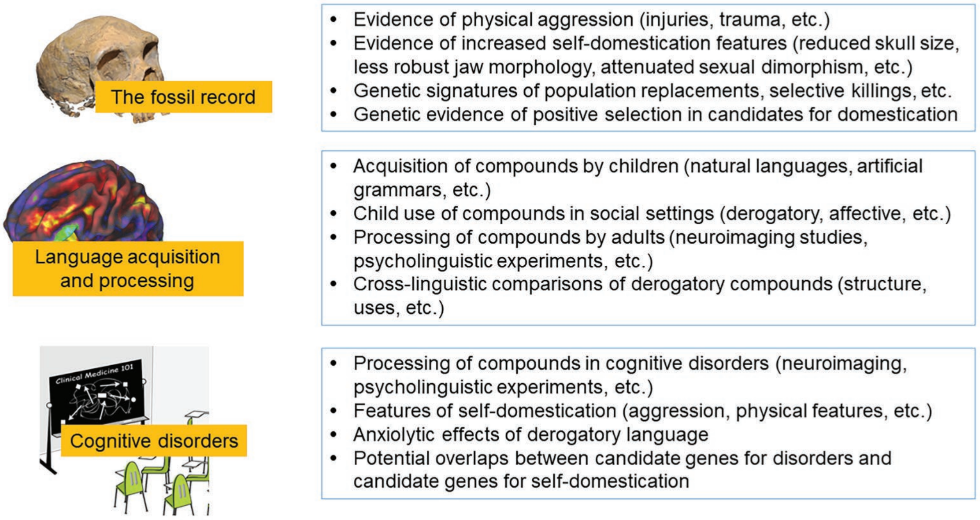

FIGURE 2 | Testing arenas for the most relevant predictions resulting from the hypothesis discussed in the paper. Image attribution: Above: "File:Neanderthal skull from Forbes' Quarry.jpg" by AquilaGib is licensed under CC BY-SA 3.0. Middle: "fMRI Image of Preteen Brain" by National Institutes of Health (NIH) is licensed under CC BY-NC 2.0. Below "File:Clinical Medicine 101 – journal.pmed.0020111.g001.png" by Daniel Mietchen is licensed under CC BY 2.5.

then this discrepancy between the two aggression types is unexpected. But the problem finds a direct solution in correlating early self-domestication processes with the emergence of simple forms of early language/grammar, as per our proposal in this paper, but also in correlating later stages of self-domestication with more complex forms of language, as discussed by Benítez-Burraco and Kempe (2018) and Kissel and Kim (2019). Given that the postulated proto-grammar is particularly suitable for expressing crude and often obscene insults, representing essentially reactive language, this kind of language would have been most useful in countering/replacing reactive aggression, but as such, it would not have affected any existing or emerging proactive aggression.

Several classes of predictions arise from our proposal, yielding specific hypotheses. We single out three such classes: (1) the history of aggression and the fossil record; (2) linguistic proxies (fossils) of the second (proto-grammar) stage in (language) evolution, and their acquisition and processing implications; and (3) Disorders and (verbal) aggression. For each of these classes, we identify some specific hypotheses that are subject to testing and falsification (see also **Figure 2**).

1. The history of aggression and the fossil record.
   i. First, we predict a gradual decrease in reactive physical aggression, accelerated during especially the second and third stages, but also continuing into the present times. This scenario already seems well supported (see e.g., Cieri et al., 2014 for the claim that features of self-domestication reached a peak at the end of Upper Paleolithic). Still, this is a hypothesis in need of further testing.
   ii. Second, we predict an increase in proactive aggression starting in the third stage, and accelerating in the fourth stage, consistent with the considerations of gradual language evolution. There is already some initial evidence for this hypothesis, as collaborative inter-group conflicts became widespread during the Neolithic (Zeng et al., 2018). But further evidence can certainly be sought to better support or falsify this hypothesis. For example, evidence of accelerated proactive aggression in the first or second stages postulated above would falsify our hypothesis and would at least necessitate a reconsideration/revision of the timeline.
2. Linguistic proxies (fossils) of the second (proto-grammar) stage in human evolution.
   i. Our first prediction is that the flatter evolutionary proxies will be acquired earlier by children, and with less effort, than their more hierarchical counterparts. As mentioned in Section "Child Development," some experiments with children already established that what we refer to here as "fossil" compounds are acquired earlier, and with more ease, than their hierarchical counterparts (Clark et al., 1986). Such experiments can be replicated with additional language proxies and conducted using additional languages, or even by using artificial grammars.
   ii. Similar expectations hold for the processing of human language by adults, where the prediction is that the processing of flatter, fossil structures, such as small clauses and compounds, in contrast to their syntactically more layered counterparts, will rely less on the more recently enhanced brain networks. Progovac et al. (2018a,b) report some preliminary results of fMRI experiments along these lines that establish clear processing differences between the two types of structures, but more studies are needed to confirm or disconfirm these results, especially cross-linguistic studies, including a variety of languages. This line of research can help determine what kind of brains are needed for the (effortless) processing of early language vs. modern languages and would potentially tie into the

considerations of the evolution of the human brain and the human skull, as discussed in section "Introduction."

3. Disorders and (verbal) aggression.
   i. The anxiolytic (stress and anxiety-relieving) properties of reactive verbal aggression are hypothesized to have contributed to the language emergence/self-domestication feedback loop. While there are proposals in the literature to the effect that tics in TS are anxiolytic (section "Tourette's Syndrome and Coprophenomena"), this should be subjected to further experimental testing. We further predict that tics accompanied by coprolalia (uncontrollable profanity) will provide better stress relief than those without it.
   ii. We make a similar prediction when it comes to automatisms in aphasia. The production of these automatisms, specifically expletives, seems to be associated with a higher degree of stress, and experiments can be designed to gauge whether such production is anxiolytic.

The truth is that very little is known about swearing and derogatory language, including its processing and genetic basis, whether in typical populations, or in disorders, most probably because this kind of language is often taboo, and typically avoided even in scientific research[24]. However, once tapped into, these phenomena, including the neuroscience and genetics of the functions and dysfunctions of swearing/derogatory language, will provide an especially fertile ground for formulating and testing a variety of hypotheses about language evolution and self-domestication, and human evolution more generally.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

LP and AB-B conceived and wrote the manuscript.

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[24] As pointed out by Freeman et al. (2009) and others, the research on coprophenomena (coprolalia and copropraxia) is very limited and leaves large gaps and many unanswered questions. The same is true of the studies of insult, swearing, and profanity more generally (e.g., Mohr, 2013; Bergen, 2016).

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Prosociality and a Sociosexual Hypothesis for the Evolution of Same-Sex Attraction in Humans

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Human same-sex sexual attraction (SSSA) has long been considered to be an evolutionary puzzle. The trait is clearly biological: it is widespread and has a strong additive genetic basis, but how SSSA has evolved remains a subject of debate. Of itself, homosexual sexual behavior will not yield offspring, and consequently individuals expressing strong SSSA that are mostly or exclusively homosexual are presumed to have lower fitness and reproductive success. How then did the trait evolve, and how is it maintained in populations? Here we develop a novel argument for the evolution of SSSA that focuses on the likely adaptive social consequences of SSSA. We argue that same sex sexual attraction evolved as just one of a suite of traits responding to strong selection for ease of social integration or prosocial behavior. A strong driver of recent human behavioral evolution has been selection for reduced reactive aggression, increased social affiliation, social communication, and ease of social integration. In many prosocial mammals sex has adopted new social functions in contexts of social bonding, social reinforcement, appeasement, and play. We argue that for humans the social functions and benefits of sex apply to same-sex sexual behavior as well as heterosexual behavior. As a consequence we propose a degree of SSSA, was selected for in recent human evolution for its non-conceptive social benefits. We discuss how this hypothesis provides a better explanation for human sexual attractions and behavior than theories that invoke sexual inversion or single-locus genetic models.

Keywords: self-domestication, homosexual, endocrine hypothesis, testosterone, sexual inversion, sexuality, bonobo

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In most contemporary human cultures that have been studied individuals who self-identify as exclusively homosexual are rare (Ward et al., 2014; Bailey et al., 2016), but a larger minority of the population report some homosexual sexual behavior and experience and a degree of same sex sexual attraction (SSSA) (Bagley and Tremblay, 1998; Savin-Williams and Vrangalova, 2013; Bailey et al., 2016). While estimates of the population prevalence and distribution of SSSA vary (Bailey et al., 2016) contemporary studies support Kinsey et al.'s (1948, 1953) conclusion that in human populations there is continuous variation in the expression of homosexuality. The variation forms a smooth cline from a large majority who report exclusive or mostly heterosexual attraction and/or behavior, through groups who report degrees of both homosexual and heterosexual attractions and/or behavior to a small minority who report exclusive homosexual attractions and behavior (Savin-Williams and Vrangalova, 2013; Bailey et al., 2016).

For evolutionary biologists SSSA and associated homosexual sexual orientation has presented somewhat of a conundrum. SSSA persists both within and across cultures (Witham and Mathy, 1985; Crompton, 2006) and within families, since sexual orientation has high heritability (Pillard and Bailey, 1998; Mustanski et al., 2005; Santtila et al., 2008; Bailey et al., 2016). Evidence from human twin studies and genome-wide genetic association studies suggest that about one third of the variation in sexual orientation can be attributed to additive genetic factors (Santtila et al., 2008; Bailey et al., 2016; Ganna et al., 2019). For evolutionary biologists the puzzle is typically posed like this: how can a heritable SSSA persist in a population when homosexual sex of itself is non-reproductive and homosexual people have fewer offspring on average than heterosexual people (Bell et al., 1981; King et al., 2005; Wrangham, 2019). There is expected to be strong selection against genetic factors that contribute to SSSA: how, therefore, can heritable homosexual attractions persist in a population (Kirkpatrick, 2000; Gavrilets and Rice, 2006; Bártová and Valentová, 2012; Rice et al., 2012; Jeffery, 2015)?

Various explanations to this puzzle have been proposed. The prevalence of SSSA is certainly too high for the trait to be maintained by recurrent random mutation (Moran, 1972). Models have consequently been proposed to explain how SSSA could be maintained in a population as a stable genetic polymorphism, but presently there is scant or no evidence to support these theories.

The theory of sexually antagonistic selection proposes that genetic factors contributing to SSSA in one sex could persist in populations if they conferred a strong selective advantage when expressed in the other sex, and various models of this kind have been posed to explain human SSSA (Gavrilets and Rice, 2006; Camperio-Ciani et al., 2008; Rice et al., 2012). Camperio-Ciani et al. (2008) explored whether the female relatives of homosexual males had more offspring than female relatives of heterosexual males, which could be indirect evidence for antagonistic sexual selection. There is some evidence that females with male homosexual relatives have more children than females with no male homosexual relatives in a Western European population (Camperio-Ciani et al., 2008; Lemmola and Camperio-Ciani, 2009), but this finding is at best only weakly supported in other populations or cultures (Vasey et al., 2007; Bailey et al., 2016; Semenyna et al., 2017), and so overall there is little evidence for sexually antagonistic selection as an explanation for SSSA in human males. No study has yet explored whether this theory might apply to human females.

An alternative hypothesis proposes that SSSA and homosexual behavior could be maintained in a population if genetic factors contributing to these traits had pleiotropic effects that conferred a reproductive advantage. Zietsch et al. (2008) explored a version of this hypothesis and reported that psychologically masculine females and psychologically feminine men typically identified as non-heterosexual, but if did self identify as heterosexual they also self-reported a greater number of sexual partners than average for heterosexuals. We note that number of sexual partners is a long way from a measure of reproductive success or fitness. We also note that a critical test of this hypothesis was whether heterosexuals with a non-heterosexual identical twin have more sexual partners than members of heterosexual identical twin pairs. Here, there was a trend in the hypothesized direction but no statistically significant difference in number of sexual partners (Zietsch et al., 2008). Zietsch et al.'s (2008) study is certainly intriguing. The data they present are compatible with a relationship between SSSA, homosexual behavior and increased socio-sexuality – a point we develop later.

Kin-selection theories propose genes promoting SSSA could persist in a population if people expressing SSSA enhanced the reproduction of relatives (Bailey and Zuk, 2009). It is assumed the indirect fitness benefit of more relatives would compensate for the presumed fitness costs associated with SSSA and same-sex sexual behavior. Invoking kin-selection theory to explain human SSSA seems a little odd. The many examples of social and reproductive traits in animals that have evolved as a consequence of kin selection emphasize the evolution of non-reproductives, not same-sex sexual behavior (Kirkpatrick, 2000). In human societies there is very little evidence homosexual people increase the reproductive output of relatives (Bobrow and Bailey, 2001; Rahman and Hull, 2005; Vasey and VanderLaan, 2012; Abild et al., 2014; Prum, 2017) offering weak empirical support to kin selection theories for SSSA. But several studies by Vasey and others have emphasized the avuncularity (defined as altruistic uncle-like behavior) and generosity of transgender males expressing SSSA (Vasey et al., 2007; Vasey and VanderLaan, 2012, 2015; Abild et al., 2014) perhaps indicating a relationship between SSSA and affiliative behavior.

Here we propose a sociosexual hypothesis for the evolution of SSSA that explores possible adaptive social functions of same-sex directed attractions and behavior. Benefits of SSSA and same sex sexual behavior for the development and maintenance of same sex social bonds and group affiliation have been proposed previously, most notably by Kirkpatrick (2000) and later by Bártová and Valentová (2012). But here we link the evolution of human SSSA to the suite of traits that evolved as a consequence of selection for ease of social integration (prosocial behavior), within-group tolerance and social affiliation. This has been described as an evolutionary process of human self-domestication (Eisenberg et al., 1983; Clay and Zuberbühler, 2011; Gleeson, 2016; Hare, 2017; Theofanopoulou et al., 2017; Niego and Benítez-Burraco, 2019; Wrangham, 2019).

Assessing SSSA in non-human animals is not easy, but what is clear is that homosexual *behavior* is not a human innovation. It is widespread in primates (Sommer and Vasey, 2006) and other animals (Bagemihl, 1999; Bailey and Zuk, 2009), and is certainly ancestral to hominids. Analyses of the contexts of occurrence of homosexual sexual behavior in primate societies suggest the behavior has various diverse functions. These include appeasement, pacification, reinforcement of social dominance structures, juvenile play, social tolerance, stress reduction, and barter (Sommer and Vasey, 2006; Clay and de Waal, 2015). Heterosexual sexual behavior shows a similar diversity of expression across primate societies (Sommer and Vasey, 2006). It appears there has been an expansion of the social functions of sexual interactions (both homosexual and heterosexual) as more complex societies evolved in primates (Werner, 2006). As a consequence, sexual behavior in primates has been subject to selection for adaptive social functions as well as the obvious reproductive functions.

Social evolutionary processes have been a major driver of recent human cognition and behavior (Eisenberg et al., 1983; Dos Santos and West, 2005); particularly selection for increased intra-group tolerance and reduced intra-group aggression (Bowles and Gintis, 2013; Hare, 2017). Prosocial individuals would have more readily accessed the fitness benefits of cooperative group living (Hare, 2017), and would have gained both greater reproductive success and social mobility (Bowles and Gintis, 2013). Enhanced tolerance also would allow for smoother integration of juveniles that moved from their natal group to a new group – bringing new ideas and technology with them. Selection for prosociality is thought to have driven the recent evolution of bonobos from their chimp-like ancestor, and proto-dogs from their wolf-like ancestor also (Hare, 2017).

In humans, dogs, and bonobos, a common suite of traits has evolved as a consequence of selection for prosociality. These are juvenilization of facial features, extended cognitive developmental periods, reduced social threat responses, reduced aggression, reduced aggressive reactivity, cooperative play behavior, and increased cooperative-communicative capacity and engagement (Hare, 2017; Theofanopoulou et al., 2017; Wrangham, 2019). This set of traits is very similar to those that have arisen from artificial selection on species for reduced aggression and fear of humans in order to domesticate them (Belyaev et al., 1985; Hare, 2017). Consequently, recent human evolution has been described as a process of self-domestication arising from natural selection for prosocial behavior (Gleeson, 2016; Hare, 2017; Niego and Benítez-Burraco, 2019; Wrangham, 2019).

Across both domesticated species and self-domesticated species it is common to see an increase in expression of same-sex sexual behavior. This is part of the expansion of the contexts of sexual behavior (same-sex oriented and heterosexual) into adult play, usually interpreted as part of an adult affiliative function for sex (Dagg, 1984; Poiani, 2011). For example, in the evolution of dogs from wild dogs, and wild dogs from wolves both self-domestication and domestication have increased expression of adult sexual play and homosexual sexual behavior relative to their wild relatives (Dagg, 1984). While domestication of livestock has not always increased rates of homosexual behavior, there are several well studied examples where domestication has yielded high levels of same-sex sexual behavior among adults (Dagg, 1984; Perkins and Roselli, 2007).

The bonobo has experienced a parallel process to humans of prosocial evolution from a chimp-like ancestor (Hare, 2017; Tan et al., 2017). Like humans, bonobos show a suite of features associated with self-domestication (Hare, 2017). Bonobos exhibit higher levels than chimpanzees of same-sex sexual behavior in contexts of adult play and social affiliation also (Clay and Zuberbühler, 2011; Dixon, 2011; Woods and Hare, 2011; Bailey et al., 2016; Hare and Yamamoto, 2017).

Same-sex sexual attraction, homosexual behavior and same sex affiliations are distinct dimensions of sexuality (Bolin and Whelehan, 2009; Jordan-Young, 2010; Greenberg et al., 2016; Valentova and Varella, 2016), but they are related. SSSA is a motivator of homosexual behavior, and sexual behavior is a strong motivator of social bonds and affiliations. Sex is a strong reinforcer of pair bonds in all social mammals studied (Young and Wang, 2004). Sexual behavior in social contexts functions as a reinforcer of social bonds also (Kirkpatrick, 2000). Same-sex social bonds are likely to be as important as heterosexual social bonds for any individual operating within a social group (Kirkpatrick, 2000). A degree of SSSA could therefore reasonably confer a selective advantage, by facilitating engagement in sociosexual behavior with the associated benefits of social reinforcement, affiliation, play, appeasement, and conflict resolution (Kirkpatrick, 2000; Bártová and Valentová, 2012). Selective benefits for SSSA could be increased ease of social bonding and reduced intragroup conflict through a willingness to engage in or initiate homosexual sexual play. Human ethnographic evidence points to an adaptive benefit for SSSA in alliance formation and maintenance (Kirkpatrick, 2000; Muscarella et al., 2005).

Mechanistic analyses indicate links between increased prosociality and SSSA. Raghanti et al. (2018) have argued that the neurochemical profile of the human striatum is unique among primates with elevated dopamine, serotonin, and neuropeptide Y signaling. They argue this feature evolved early in hominid evolution and increased sensitivity to social cues to promote empathy and affiliative behavior (Raghanti et al., 2018). Self domestication in both dogs and humans is believed to have caused evolutionary changes in serotonin, oxytocin and androgen systems that regulate affiliative, threat, and aggressive behavior (Hare, 2017), and are involved in chimpanzee social affiliation (Samuni et al., 2017). These are the same endocrine systems that have been implicated in the development of human SSSA and homosexual behavior (Mustanski et al., 2002; Balthazart, 2011; Fleischman et al., 2015). In domesticated sheep changes in these neurochemical systems have been considered causal of increased levels of homosexual behavior (Perkins and Roselli, 2007). Taken together, these studies suggest an overlap between the neurochemical systems involved in affiliation and prosocial behavior and those involved in an increased incidence of same-sex sexual behavior in animals. Such a relationship is expected given that sex is itself a mechanism of social bonding in mammals (Young and Wang, 2004; Young et al., 2005).

Prosociality, increased in-group tolerance and increased social affiliation: these are extremely complex traits involving widespread changes in behavior, anatomy, and neurophysiology (Hare, 2017; Theofanopoulou et al., 2017; Raghanti et al., 2018). Genetic changes underlying the evolution of such traits are likely to be complex and highly polygenic. Presently not much is known about the genetic basis of human SSSA, but as we learn more about it, it is clear human SSSA is also highly polygenic and a complex multicomponent trait (Mustanski et al., 2005; Prum, 2017; Sanders et al., 2017; Ganna et al., 2019; Swift-Gallant et al., 2019). The high heritability of human SSSA is caused by a large number of genes each with individually small effect. These genes likely contribute to different aspects of sexuality which can assort independently (Mustanski et al., 2005; Sanders et al., 2017; Ganna et al., 2019). Genetic models for the evolution of human SSSA should therefore reflect this complexity and be polygenic and multicomponent, rather than positing individual genes of large effect, as has occurred previously (Gavrilets and Rice, 2006; Rice et al., 2012).

A polygenic and additive genetic model of SSSA is compatible with the nature and distribution of SSSA in human populations, which features continuous variation in the degree of SSSA from a majority reporting exclusively heterosexual attractions to a small minority reporting exclusively homosexual attractions (Bailey et al., 2016). Along this cline of variation individuals expressing degrees of both homosexual and heterosexual attractions are stable sexualities and not transitional forms (Bailey et al., 2000; Diamond, 2008; Rosenthal et al., 2012; Savin-Williams and Vrangalova, 2013). We propose this pattern of variation could have arisen from selection for prosociality increasing the frequency of alleles in a population across multiple loci that contribute to prosocial behavior. This would include alleles contributing to SSSA because of the benefits of sociosexual same-sex behavior for same-sex social bonding and affiliation. If a trait is highly polymorphic and polygenic [as sexual orientation seems to be (Sanders et al., 2017; Ganna et al., 2019)] the random recombination of genes in sexual reproduction would result in a spectrum of heritable variation for strength of SSSA in a population (Prum, 2017).

Given this argument one might ask why SSSA is not more common in human populations. Indeed, Kirkpatrick (2000) wondered that bisexuality might be an adaptive optimum since it would allow for sociosexual affiliative behavior with members of both sexes. Kirkpatrick (2000) proposes that any reproductive disadvantage from a low level of same-sex sexual behavior could be minor or negligible, irrespective of the degree of SSSA associated with the behavior.

To this point we note simply that while individuals reporting exclusive SSSA are rare in most contemporary human populations, SSSA is not. While specific measures vary all studies recognize that males and females reporting some degree of SSSA are relatively common, and not rare (Kinsey et al., 1948, 1953; Kirkpatrick, 2000; Mustanski et al., 2002; Bailey et al., 2016). Bisexuality is more common than homosexuality, but the nature of variation in SSSA is often not well appreciated since experimentalists are prone to force a binary dichotomy across what is in reality continuous and multivariate variation in sexuality (Jordan-Young, 2010). There may also be cultural reasons why the degree of SSSA in populations may go under-reported.

We emphasize that our hypothesis is not that homosexual people are domesticated, or even more prosocial than the population average. Rather, we recognize that self-domestication has been an important process in the recent evolution of our species as a whole. SSSA has increased in frequency in humans as a consequence of the self-domestication syndrome experienced by our species. If correct, this sociosexual hypothesis comprehends the phenomenon of human SSSA as part of broader adaptive prosocial changes in recent human cognitive and social evolution (Burkart et al., 2009, 2014; Hare, 2017).

Two other authors have remarked on a link between SSSA and selection for prosociality: Prum (2017) and Wrangham (2019). Prum (2017) argues that for humans female dispersal was the ancestral condition, with females rather than males leaving their natal group. He proposes that female SSSA could evolve as part of selection for female prosociality to aid female introgression into a new social group and strengthen female-female social bonds (Prum, 2017, p. 508). He further argues that male SSSA and homosexual behavior could have evolved through female mate choice (Prum, 2017). Females may have preferred males that show a degree of SSSA since this male trait would lessen the intensity and investment of males in sexual and social control of females, and would subsequently have fostered the evolution of prosocial males and more cooperative male–male and female–male relationships (Prum, 2017, p. 509).

Wrangham (2019) has also recognized an association between prosociality and homosexuality, but Wrangham proposes a very different hypothesis for why this association might be so. Wrangham (2019, p. 189) suggests human homosexuality is a maladaptive by product of selection against reactive aggression in humans. Wrangham (2019) argues that selection for reduced reactive aggression reduced prenatal testosterone levels in males, which resulted in a maladaptive expression of homosexuality in a minority of males.

Models of human evolution are naturally hard, if not impossible, to prove or disprove, but here we note that Wrangham's explanation for an association between homosexuality and prosociality does not, and cannot, explain homosexuality in women. By contrast, prosocial benefits of SSSA would be expected to apply to both female–female social relationships and male–male social relationships (Kirkpatrick, 2000). Prum's (2017) evolutionary argument is interesting in many ways, not least of which is because it proposes different (but interacting) selective pressures for the evolution of male and female SSSA in humans. Here we have argued a link between prosocial evolution and SSSA. Prum (2017) recognizes this selective force for females, but considers female mate choice the primary driver of human male SSSA, with prosociality in human males an outcome of female mate choice. This hypothesized evolutionary scenario is perhaps more complex than ours, but that does not mean it is less likely. If non-prosocial species could be found in which female mate choice had lead to the evolution of male SSSA this would lend strong support to Prum's (2017) model for social evolution.

Wrangham's reasoning and evidence draw on the endocrine hypothesis for human homosexuality, which has been strongly refuted (Jordan-Young, 2010). There are many variants of the endocrine hypothesis, but they all propose that SSSA is caused by some malfunction or gendered misexpression of endocrine systems considered responsible for establishing gender-typical behavioral differences between heterosexual males and heterosexual females (Mustanski et al., 2002; Balthazart, 2011; Rice et al., 2012; Bailey et al., 2016). Hypotheses vary as to when or how in development a change in endocrine systems could result in SSSA. Arguments in support of the endocrine hypothesis come from a range of experimental manipulations of mammals, including primates, which demonstrate a role for androgens in the organization and development of male and female typical sexual and social behavior, and also show that severe manipulations of endocrine systems in early development can result in males showing female-typical sexual behavior and vice-versa (Balthazart, 2011; Poiani, 2011).

The endocrine hypothesis does not, however, fit well to features of human SSSA (Jordan-Young, 2010). The example of female congenital adrenal hyperplasia (CAH) is often cited as evidence supporting an endocrine basis of human SSSA (Balthazart, 2011). This disorder causes prenatal hypertrophy of the adrenal gland, and consequently the developing fetus is exposed to higher than normal levels of testosterone. Females with CAH report a higher incidence of adult homosexual orientation than that of the population as a whole, but most females with CAH report exclusively heterosexual attraction (Meyer-Bahlburg et al., 2008; Jordan-Young, 2010). This would suggest that for women there is not a simple relationship between elevated prenatal testosterone and SSSA. Further, in both animal studies and the human cases of CAH pre- or perinatal endocrine manipulations have consequences for the development of anatomical secondary sexual characteristics and genital morphology. Female rhesus monkeys given testosterone postnatally develop an enlarged clitoris (Pfaff, 1999; Dixson, 2013) and some females with CAH also develop partially masculinized genitalia (Bailey et al., 2016). There is no evidence that homosexual people (male or female) have intersex genital development (Jordan-Young, 2010; Bailey et al., 2016) suggesting it is unlikely an endocrine imbalance pre or perinatally is causal of human SSSA.

Rice and Gavrilets (Rice et al., 2012) argued that a misexpressed epigenetic modifier of testosterone sensitivity or insensitivity that affected development of the brain only and not the body and genitals might possibly explain why homosexual people show SSSA but do not have intersex bodies. This is an interesting theory, but there is currently no evidence such a precise epigenetic modifier of testosterone sensitivity exists in either humans or other animals.

However, it is proposed, the endocrine hypothesis effectively categorizes homosexuals as partially intersex: homosexual men as partially feminized and homosexual women as partially masculinized (Mustanski et al., 2002; Balthazart, 2011). Such a portrayal of homosexuality perpetuates discredited ideas of homosexuality as sexual inversion (Ellis and Symonds, 1896), and the historic medical and psychological view of homosexuality as pathological. These views of homosexuality have long since been rejected by clinical and social psychology because in clinical psychology they have been found to be inaccurate, unsupported, and unconstructive (Haumann, 1995; Jordan-Young, 2010; Bailey et al., 2016). We argue that it is time for evolutionary psychology to also question the veracity of the endocrine hypothesis for human homosexuality.

Our proposed hypothesis for human SSSA has no requirement for sexual inversion. It would not require that SSSA be masculine-like for females or feminine-like for males. Rather, consideration of both an additive genetic model for SSSA and selection on SSSA in prosocial contexts would predict a diversity of expression of SSSA in both males and females.

We have argued that SSSA evolves as part of selection for increased prosociality. This hypothesis is testable. If it is correct there should be a detectable benefit to SSSA in contexts of within-group cohesion or cooperative tasks. Some evidence already points to a relationship between affiliation and SSSA in humans. Kirkpatrick (2000) documents ethnographic examples of SSSA and homosexual behavior strengthening important social affiliations in both males and females and SSSA supporting long term supportive social bonds. Human males self-reported a higher level of homoerotic motivation if they were primed with words related to friendship than if they were primed with words related to sex (Fleischman et al., 2015). This suggests that for males social affiliation is a greater releaser of SSSA than a sexual context (Fleischman et al., 2015). Whether within-group SSSA *enhances* cooperation and group performance to provide individual selective benefits remains to be tested, however.

Animal models could provide a powerful resource to explore these questions. We have described how homosexual behavior is more common in highly prosocial species than non-prosocial close relatives. We would predict homosexual behavior to enhance cooperation, group cohesion and performance and ultimately increase the reproductive success of individuals that are part of a high-functioning group in animals also. Comparing the consequences of homosexual behavior in bonobos and chimpanzees for group function would be a test of this hypothesis (Moscovice et al., 2019).

If the sociosexual hypothesis of SSSA evolution is correct we would expect to see an introgression of systems causal of human SSSA and social and affiliative behavior at both genetic and physiological levels of analysis. As we have discussed above, current evidence is compatible with this hypothesis, but significant gaps remain in our understanding of the genomic and neurophysiological basis of human sexual orientation and much work remains to be done.

Exploration of human SSSA has thus far been dominated by assumptions that the trait must be maladaptive (Bell et al., 1981; King et al., 2005; Wrangham, 2019). It may be timely and beneficial to explore alternatives that consider the sociosexual adaptive functions of same sex attraction and sexual behavior, and the full spectra of expression of SSSA.

AUTHOR CONTRIBUTIONS

AB and BH conceptualized and wrote the manuscript.

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Prehistoric Perspectives on "Others" and "Strangers"

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Social "connectivity" through time is currently considered as one of the major drivers of cultural transmission and cultural evolution. Within this framework, the interactions within and between groups are impacted by individuals' distinction of social relationships. In this paper, we focus on changes in a major aspect of social perceptions, "other" and "stranger." As inferred from the archaeological record, this perception among human groups gained importance during the course of the Pleistocene. These changes would have occurred due to the plasticity of cognitive mechanisms, in response to the demands on behavior along the trajectory of human social evolution. The concepts of "other" and "stranger" have received little attention in the archaeological discourse, yet they are fundamental in the perception of social standing. The property of being an "other" is defined by one's perception and is inherent to one's view of the world around oneself; when shared by a group it becomes a social cognitive construct. Allocating an individual the status of a "stranger" is a socially-defined state that is potentially transient. We hypothesize that, while possibly entrenched in deep evolutionary origins, the latter is a relatively late addition to socio-cognitive categorization, associated with increased sedentism, larger groups and reduced territorial extent as part of the process of Neolithization. We posit that "others" and "strangers" can be approached from contextual archaeological data, with inferences as regards the evolution of cognitive social categories. Our analysis focused on raw material studies, observations on style, and evidence for craft specialization. We find that contrary to the null hypothesis the archaeological record implies earlier emergence of complex socio-cognitive categorization. The cognitive, cultural and social processes involved in the maintenance and distinction between "others" and "strangers" can be defined as "self-domestication" that is still an on-going process.

Keywords: social behavior, paleolithic archaeology, socio-cognitive construct, social stereotypes, inter-group relationships, material culture proxies

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> *"No man is an island entire of itself; every man is a piece of the continent, a part of the main;"*
> MEDITATION XVII, Devotions upon Emergent Occasions (*John Donne*)

INTRODUCTION

While much research focused on the question of the emergence of "modern" cognition – a vague concept that is variably understood and therefore variably recognized (see, e.g., Belfer-Cohen and Hovers, 2010) – there is a growing realization that rudimentary forms of human cognition can be traced into deep prehistoric times (e.g., Deacon, 1989; Laland, 2017 and references therein).

Research into human biological and social evolution has attempted to identify the role played by various cognitive aspects (e.g., Donald, 1993; Richerson and Boyd, 2000; van Schaik and Pradhan, 2003; Dunbar and Shultz, 2007; Andersson, 2011; Wynn and Coolidge, 2011, 2016; Grove, 2012; Jaffers, 2014; Dennett, 2016; Lombard and Gardenfors, 2017). Archaeologists of early prehistory directed their attention to the production and use of stone tools, focusing on planning depth, dexterity, and forms of teaching and learning. At the same time, primatologists, prehistorians, and paleoanthropologists developed lines of inquiry that focused on the capacity of the hominin brain to create, maintain and augment social relationships (e.g., Delagnes and Roche, 2005; Stout et al., 2008, 2011, 2019; Nowell and Davidson, 2010; Vaesen, 2012; Dunbar et al., 2014; Tomasello, 2014; Tomasello and Call, 2014; Dunbar and Shultz, 2017; Gärdenfors and Högberg, 2017; Herzlinger et al., 2017).

Plasticity of cognitive mechanisms is implicated as a major factor responsible for behavioral and cultural trajectories, as it both influences *and* is influenced by the way those have evolved over the course of prehistoric time. In fact, it seems unlikely that culture could have evolved without affecting cognition. Colagè and d'Errico (2018):4) argued that " . . .the brain [modifies] physiological, functional, and/or structural features as a consequence of experience and practice without any concomitant change at the genetic level" (see also discussion in Lotem et al., 2017).

In this context, the emergence of human sociality (Barrett et al., 2012) draws our attention to "social cognition" (SC) which emerges as an important element that influenced the structure, economy and culture of Paleolithic groups (e.g., Davies, 2016). SC constitutes people's subjective interpretations of social situations as well as the concepts and cognitive processes whereby they were shaped (Korman et al., 2015; and see Thompson et al., 2016). Because of the assumed link between culture and SC, we also speculate that changes in cognitive social concepts, and thus in social relations, can be inferred from the cultural record of the Pleistocene.

The general question as to how prehistoric hominins structured their social relations is not a new one. Two fundamental, widely-discussed concepts in paleoanthropological research are those of "group" and "population" (e.g., Birdsell, 1958; Zhou et al., 2005; Gamble et al., 2014; White, 2017; Casari and Tagliapietra, 2018; and references therein). Attention was devoted to the variable forms of the organization of individuals into groups as the mechanisms that enabled rich and complex social configurations in extant and past hunter-gatherers (e.g., Grove, 2010; Hill et al., 2011; Grove et al., 2012; Bird et al., 2019; Domínguez-Rodrigo et al., 2019; Herzlinger and Goren-Inbar, 2019; Malinsky-Buller and Hovers, 2019).

In particular, shifts in group size and intra- and inter-group connectivity are currently considered as significant drivers of cultural transmission and cultural change (e.g., Premo and Scholnick, 2011; Derex et al., 2014, 2018; Stout, 2018; Greenbaum et al., 2019). The interactions within- and between- groups are complex processes that are impacted by the social roles of the individuals that comprise those units (Jenkins et al., 2018; Cacault and Grieder, 2019). These encompass the self-recognized place of an individual within her group, which in turn shapes ". . . the processes of formation of groups and changing membership of groups." (Festinger, 1954: 135).

Here we discuss the SC concepts of "other" and "stranger," fundamental in defining social interfaces within and between groups of hunter-gatherers, as they have shaped, to considerable degree, economic, mobility and territorial behaviors that can be inferred from the archaeological record. Yet, these concepts have rarely been addressed in archaeological discussion.

In the modern (and, mainly, post-modern. . .) discourse, "other" and "stranger," are often used alternately. However, they are not synonymous. Dictionary definitions run:

"Other" – refers to a person or thing that is different or distinct from one already mentioned or known about[1].

"Stranger" – a person who does not know a particular place or community or is not known in a particular place or community[2].

Addressed from contextual archaeological data, our exploration is preliminary and inherently speculative, with inferences as regards the evolution of human sociality. As a caveat to the discussion we must add that the nature of prehistoric evidence clearly impedes archaeologists from discussing the socio-cultural process defined by cultural anthropologists and sociologists as "othering" or the concept of "The Other".

The human social cognition system reflects the history of the genus *Homo*, potentially as far back as *Homo erectus* (∼1.8 million years ago), during which SC played a major part in constructing the human unique "niche" of adaptation to the external world (Laland et al., 2014; Davies, 2016). It seems to us that from the very beginning humans, "a highly intelligent creature who is tuned to the world's complexity" (Davies, 2016:104), interacted with friends, "others," "strangers," and even family, through cultural "tool kits." The latter would include shared social norms, predispositions and prejudices, being aware that "we are differently located in a shared world." (*ibid*.). The active role of culture in shaping the social landscape of humans, in conjunction with genetic dictates and sometimes over-riding them, constitutes what one might define as "self-domestication."

The property of "otherness" is inherent to one's view of the surrounding world and to a large degree defines oneself (see definition above). In evolutionary terms the notion of being an "other" is an innate trait of human sociality, and is immutable. At a group-level, when a number of individuals consider themselves as "one," vis-à-vis individuals or groups that do not belong to the "one," "others" becomes a social cognitive construct. Still, there are degrees of social "otherness" that can be perceived within and between groups. Hunter-gatherer kinship terminologies (Chapais, 2014) make it psychologically possible to embrace non-kin members of one's residential or task group, with whom one shares common history and beliefs, in order to accept them as kin. For example, Bird et al. (2019: 102), describing the Martu in the Western desert of Australia, state: "Many of the compound families in the 2005 census were actually multigenerational extended "classificatory kin" (e.g., older and younger "sisters"

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[1] https://en.oxforddictionaries.com/definition/other

[2] https://en.oxforddictionaries.com/definition/stranger

who share the same fictive kinship section, and are thus parallel "cousins", but may have no close biological relationship)."

The concept of "stranger"is a trait of a complex society, an *emergent* social construct that is transient, since it depends on changeable cultural perceptions. In the words of Korman et al. (2015: 31), "This constant and reflexive updating of mental states presents a significant computational challenge, and people's ability to conduct such rich and dynamic social interactions is one of the greatest achievements of human cognition."

A SUGGESTED DIACHRONIC SCENARIO

Some non-human primates appear to present behaviors that suggest that they may differentiate between "others" and "strangers." To wit, the viability of a chimpanzee genetic pool (which is $\leq$300 individuals) is maintained by the relocation of fertile females among groups. When chimpanzees from those groups ("kin" or "others" in our terminology) encounter each other, the outcomes vary from skirmishes to friendship (see Tokuyama et al., 2019 for a recent discussion). This contrasts with encounters of groups from a different breeding pool ("strangers"), who fight until annihilation of one of the groups, including productive females.

Even when leaving aside the question of how deep the evolutionary roots of ape/chimpanzee aggression behavior might be (e.g., Ferguson, 2011; Sussman, 2013), there are a number of compelling arguments to support the view that the survival of human groups depended on the existence of social groupings of non-kin, even beyond "classificatory kinship" relationship. Viable mating networks, constituting some hundreds of individuals, are perhaps the most obvious such social units, within which interactions among "others" took place. Additional incentives for interacting with non-kin "others" may have involved the need to outcompete carnivores and gain safety through numbers. In many ecological contexts, low carrying capacity would preclude protracted and/or large aggregations, such that early hominins spent most of their time in small residential groups within an overall larger, even if mostly virtual, social structures (e.g., "extended groups," Gamble, 1999). The latter constituted the pool for the "daily" grouping, enabling a flexible fission-fusion social structure, which was in turn constrained by ecology, technology and demography (Grove et al., 2012). Cautiously drawing inferences from extant populations, it is reasonable to assume that aggregations, namely large meetings that provided networking opportunities, were not random, as they had to be part of a basic behavioral routine, for example seasonal/annual aggregations, obligate exchange, etc. (e.g., Hovers, 1990; Bar-Yosef, 1997; Pearce and Moutsiou, 2014).

The frequencies of large group gatherings were dictated by population densities, such that lower densities would require more frequent aggregations. These meetings would have been of a limited duration. The reasons could be shortage of resources to sustain relatively large numbers of people. Since the meetings were scheduled, of a short duration and in an agreed-upon territory, there would be fewer opportunities for encroachment on the resources of the respective groups taking part in the aggregation. In ethnographic contexts, the fissioning of the aggregation stems from rising social tensions rather than environmental stress. When asked how people knew when to break up an aggregation, a !Kung informant replied that it happened when the women had no further information to share and started quarreling at the communal water hole (Konner, 2002).

Under these circumstances members of a particular group were likely aware of "us" or "we", i.e., their own group members, as opposed to "others" with whom they had relatively brief social interactions. Under Paleolithic conditions (of sparse populations, spread over extensive territories) there would be only "us" and "others," because every person, with whom one had any kind of interaction, belonged by default to the same reproductive network, even if not of the same basic social unit (extended family, kin and classificatory kin, residential unit). At all times, these social interactions involved kin and "others" but not "strangers."

Because of the strong influence of culture on SC, changes in economic, demographic, spatial (and other) aspects of human culture introduced changes in perceptions of social relationship, i.e., in SC. Through time, one can observe a rise in residential group size and a reduction in territory sizes – both linked to improved means of production and associated demographic changes (Hayden, 1981; Gilman, 1984; Hamilton et al., 2007a,b). A larger group could serve as a viable genetic pool nearly on its own, without the need to meet members of other groups on a regular basis. Moreover, evolving complex societies would become more tethered to their geographic locations and more protective of their bounded resources and, in later periods, their surpluses. Encounters with individuals that did not belong to the same group would be less crucial for survival, and therefore would not be pre-scheduled or repetitive. On the other hand, when such encounters occurred, potential causes for inter-personal tensions would stem from economic interests, related to the availability, ownership and sharing of resources. Such encounters occurred between "strangers," i.e., individuals or groups that did not share common history, cultural traditions, or behavioral patterns.

With the increase of global and local population sizes and change of economic mode, with the introduction of farming/agriculture, boundaries became less defined by clear-cut geographic features. Instead, "crowding" (e.g., by sedentism ensuing increased population densities) led to the emergence of socially constructed barriers. The definition of "strangers" lost its dependency on rare, random encounters. People came to consider as strangers also individuals they could meet on a daily basis but belonged on the other side of the social barrier.

The perception of "strangers" became even more nuanced through time. As networks of exchange (of both commodities and information) expanded, the rate of encounters with strangers increased, being beneficial to both sides. Under this premise some strangers, whose expertise and fields of knowledge complemented the ones present within a group, would be favored and would be more often tolerated by, if not accepted into, a given community. This differentiation became most obvious with the introduction of craft specialization and market economy. Hence it is in these later periods that we expect to find indications for "strangers" in the archaeological record.

The scenario presented above relies on theoretical, sociological and ethnographic knowledge, all engaged by researchers in attempts to structure a narrative of the evolution of human society and sociability. We find similarities with the question of children's visibility in the archaeological record, a topic that, once raised, has burgeoned into a prolific field of inquiry (see, for example, Hammond and Hammond, 1981; Shea, 2006; Baxter, 2008; Chappell et al., 2013). The challenge herewith would be to evaluate the feasibility of archaeology to provide evidence based on the material culture record for the suggested scenario of the diachronic transformation of SC as regards "others" and "strangers." On the evolutionary scale of prehistory, our questions should be formulated at the group rather than individual level.

THE ARCHAEOLOGICAL EVIDENCE

An obvious question is which archaeological proxies can be used in addressing such questions. Given the scenario above, we suggest investigating aspects of the archaeological record that are often understood as markers of personal and group boundaries and alliances. Prominent among these are elements that denote territoriality, social identities, and within- and between-group relationship. Here we address examples from pertinent behaviors identified archaeologically.

The types of **raw materials** and their distributions within and between regions speak to the modes of procurement and transport and help to understand spatial dimensions of group interactions. At least in some instances, it is possible to discern between direct procurement (i.e., when a person/group traveled to the source and brought material back to a site) and forms of exchange. Each of these behaviors potentially bears implications for the type of interactions between groups in a given geographic space, namely, contacts with "others" or with "strangers."

Stylistic variations within various categories of material objects have been argued to represent social identities at personal, group and regional levels. In some instances, stylistic variability can be tied to the fission-fusion social structure dynamic, specifically to the phase of aggregation when many "others" come together. It is sometimes possible to identify stylistic particularities that were used consciously as emblems, specifying group or population identities. By default, the absence of a shared emblem would denote one's state of "stranger."

The phenomenon of **craft specialization** pertains to differences in both style and production technology. Whereas experts perform with high levels of both conceptual and practical (*savoire-faire*) knowledge, average or novice practitioners possess the theoretical knowledge that is embedded in their material culture traditions, but would implement it poorly. Hence these two (broad) categories of skill are identified archaeologically (e.g., Karlin et al., 1993).

In a number of published case studies, the signature of local experts, who adhere to the raw materials, technological practices and styles of their group, has been recognized. Conversely (in particular during later prehistory) there are instances when the material record suggests that an artisan was not local, as expressed by the use of technology and style that had emerged and developed elsewhere. This would suggest a different type of social standing within the group, that of a "stranger."

As our archaeological experience lies mainly within the Levantine record, we discuss some of the implications of the above scenario by looking closely at the details of selected case studies from the Levant. Our insights from the regional record are then contextualized into a broader geographic scope in the Discussion.

Raw Material

In the Levant (**Figure 1**), flint is the nearly exclusive raw material used for making stone tools (Goring-Morris et al., 2009). Its ubiquity on the landscape suggests that throughout time the optimal behavior of Levantine hominins was that of local procurement from nearby sources of suitable flint, embedded in their subsistence system. This pattern characterizes many Eurasian Paleolithic groups (e.g., Geneste, 1985; Féblot-Augustins, 1993, 2009). It has even been suggested that the same raw material sources/quarries had been recognized and utilized over tens of thousands of years (Gopher and Barkai, 2014; Finkel et al., 2019). If that scenario holds, it would suggest that (for each period) such locations may have served as places of meeting between "others," i.e., individuals that belonged in a single mating system.

However, studies of raw material-related behaviors among Middle Paleolithic (MP; ca. 250,000–50,000 years ago) groups in the Levant suggest that hominins (both Neanderthals and modern humans) did not always opt for a "least effort" solutions for raw material requirements. At times, they obtained a variable (across sites) fraction of the raw material from additional, diverse sources, some of which were located at relatively long distances from the habitation sites. At Amud Cave (**Figure 1**; ca. 68,000–55,000 years ago), for example, this entailed a relatively significant, though non-systematic, transport from numerous, different sources located at distances of over 60 km. Notably, the techno-typological traits and the way of using the "exotic" raw material do not differ from those of the local flint, suggesting that the same people used the local and non-local sources (Ekshtain et al., 2017). Unexpectedly, the existence of a "buffer zone" in the central Galilee, located midrange between the local and the most distant outcrops, was revealed by this analysis. This zone remained unexploited by the Amud hominins, even though it contained many flint outcrops of reasonable quality (Ekshtain, 2015). The appearance and distribution of non-local raw material behavior in the Amud Cave assemblages can be interpreted as the outcome of direct procurement from distant sources. This would potentially entail encounters with groups of "others" within the same mating system. It would constitute an example of permeable social boundaries and the inclusion of the "other" within the economic and cognitive realm of the group. However, the presence of a "buffer zone" possibly demarcates a rigid boundary between groups that perceived each other as "strangers."

FIGURE 1 | Map showing the location of sites mentioned in the text. Base map from Google Earth.

The notion that the construct of "strangers" was activated in the social cognition of MP hominins gains support from another case study at the open-air site of 'Ein Qashish (**Figure 1**; ca.70,000–60,000 years ago). Lithic raw materials were imported into the site from both local and more distant sources. Interestingly, the site's occupants seem to have avoided exploiting available, good-quality sources located east of the site (Ekshtain et al., 2014). This pattern could not be explained through strictly economic aspects of raw material organization. Thus, Ekshtain et al. (2014) suggested that the decision of 'Ein Qashish hominins to avoid exploitation of these sources speaks to social/cultural constraints imposed by territorial boundaries (e.g., Wilson, 2007) between groups identifying themselves as "strangers" to each other.

The different implications for social cognitive distinctions, associated with direct transport vs. indirect procurement through exchange, may be best considered when dealing with raw materials from distinct geographic sources. In the Levantine record, this can be done by looking at marine shells. Such items are known from MIS 5 (ca. 120,000–90,000 years ago) in Qafzeh and Skhul caves (**Figure 1**; Vanhaeren et al., 2006; Bar-Yosef Mayer et al., 2009) as well as in the later open-air site of 'Ein Qashish (70,000–60,000 years ago) (Ekshtain et al., 2019). The relative proximity of the sites to the Mediterranean shorelines of their respective times of occupation and the sporadic appearance of shells in the relevant assemblages likely reflect direct transport rather than exchange (Bar-Yosef Mayer et al., 2009; Hovers, 2009), seemingly within the territory of a mating network (i.e., "others").

A later example from the Epi-Paleolithic (24,000–11,500 years ago) site of Urkan e-Rubb IIa (**Figure 1**; ca. 17,000 years ago; Hovers and Marder, 1991) requires a more nuanced consideration. Located in the Jordan Valley, this site was a place of bead production, to which shells of selected genera and species were brought unmodified, cut and made into beads *in situ*. Because of the distance from the contemporaneous shoreline of the time (some 70 km to the west), and because of the large number of shells found in Urkan, this situation could be construed as indicative of exchange between groups, reflecting contacts with "strangers" beyond the group's habitual territory. Two lines of evidence suggest differently: first, among the shells that reached the site very few belong to species that were not part of the repertoire of Epi-Paleolithic groups (Hovers et al., 1988; Bar-Yosef Mayer, 2005). These shells seem to have been collected due to mistaken identification. If the Urkan shells were retrieved by exchange, it is likely that the mistake would be discovered during negotiations. Thus, these specimens reflect collectors' error, indicating that the site's occupants themselves traveled to the shores of the Mediterranean. Moreover, the lithic assemblage of Urkan bears striking similarities to those from sites located in a specific part of the east Mediterranean coast (Hovers et al., 1988; Hovers and Marder, 1991). In the present context of discussion, the archaeology seems to imply that the occupants traveled to the shoreline within their own territory, and that they encountered "others," rather than "strangers."

Style

Stylistic characteristics are widely accepted as expressions of individual or group identity (Sackett, 1990; Hegmon, 1992; McElreath et al., 2003; McGuire and Hildebrandt, 2018; see papers in Wobst, 1977; Stark, 1998). To bear on the cognitive differentiation between "other" and "stranger" at the population level, we turn to a striking example of its expression in the Levantine record.

The "Levantine Aurignacian" is a short-lived (37,000–34,000 years ago) cultural entity that existed only in the northern part of modern Israel and along the Lebanese coast. It is a unique phenomenon in the Upper Paleolithic (UP; 48,000–24,000 years ago) sequence of the Levant in that it shows greater similarity to the West European "classic Aurignacian" cultural entity (dated there to ca. 40,000–27,000 years ago) than to the local archaeological entities that immediately precede or follow it (Belfer-Cohen and Goring-Morris, 2014). This similarity is seen in both its chipped stone typo-technology and its non-lithic objects. Among the latter are personal ornaments such as tooth pendants as well as bone and antler worked items (Goring-Morris and Belfer-Cohen, 2006). Both the European Aurignacian and the Levantine Aurignacian shared complex technical concepts of antler working as opposed to simpler bone-working technologies.

A unique feature of the Levantine Aurignacian is the occurrence of notched bones (n = 15; typically, gazelle scapulae as well as a single hyoid bone) from the Aurignacian levels of Hayonim, Manot, Kebara (and possibly Emireh) caves (**Figure 1**), all located in northern Israel. Contrary to European Aurignacian sites, where similar items were reported as sporadic finds per site/assemblage, the assemblage from Hayonim Cave is relatively large (n = 9; Tejero et al., 2018). A careful technological analysis demonstrated that the notches constitute intentional markings. Whereas other modified bone objects in the same assemblages, mainly awls and "chisels" intended probably for mundane use, were minimally modified, the notched scapulae were shaped through a complex and specific technique, rarely observed in the Aurignacian techno-complex in Europe.

The difference between the Levant and Europe *vis*-a-*vis* notched items is expressed in the selected animal taxa, the raw materials and anatomical elements used, and in the types of "decorated" objects. In the European Aurignacian notches were made on bone, antler and ivory pieces deriving from reindeer, red deer, bovid, and mammoth; the marks occur on antler, bone splinters, personal ornaments and on "utilitarian" tools such as polishers. In contrast, notched pieces in the Levantine Aurignacian are highly uniform and homogenous, with gazelles being the only animal species selected and with an almost exclusive use of a single anatomical element, the scapula.

The standardization of their production procedures as well as their relative concentration in Levantine Aurignacian assemblages indicate that these items were unique features of the regional record. It was suggested that they served as an emblem of the Levantine Aurignacian (Tejero et al., 2018). Such items possibly reflect the strong ties between various Levantine Aurignacian communities by serving as a marker of "us" and "others" (i.e., biological and "classificatory" kin), differentiating them from the surrounding population of "strangers" (e.g., the native Ahmarian cultural entity)[3], who did not share the social and cultural worldviews expressed through this particular cultural item.

Tooth pendants, recovered from the very same sites of the short-lived Levantine Aurignacian, illuminate another facet of the social cognitive distinctions between "others" and "strangers." By way of example, we use the assemblage from the same layers at Hayonim Cave (Belfer-Cohen and Bar-Yosef, 1981). In contrast to the notched pieces, tooth pendants were never made on gazelle teeth, but on the vestigial canines of (mostly) male red deer (*Cervus elaphus*), and were shaped by a particular technique. Both the manufacture marks and the use-wear signs point toward personal ornaments. Some of the modification processes differed from those observed in other Levantine Aurignacian sites (Tejero et al., submitted).

In the European Aurignacian record, the exploitation of mammal teeth – including in some cases human teeth – became a common practice, probably playing a role in the symbolic sphere of these hunter-gatherer groups. Different teeth (incisors, canines, premolars and molars) of a large spectrum of herbivores (e.g., reindeer, red deer, horse, bison, goat) and carnivore (e.g., bear, wolf, fox) species were selected for the manufacture of these ornaments. The flexibility seen in the techniques employed for ornament production is expressed by the emergence of region-specific (albeit interconnected) characteristics (Vanhaeren and d'Errico, 2006).

The use-wear of the Levantine and European Aurignacian pierced teeth implies identical utilization of the objects, suggesting shared symbolic practices. The *in situ* production of the pendants, demonstrated at least for some of the Hayonim items, reinforces this suggestion. This contrasts significantly with the archaeological manifestations of the locally-rooted Ahmarian techno-complex. Thus, accepting that the pendants were markers of the Aurignacians, their similarity in the Levant and in Europe is striking. It lends support to the notion of the Levantine Aurignacian as an incursion from Europe that is linked to its geographic origins through cultural tradition. The pendants therefore suggest that the Aurignacian populations were "others" within a Mediterranean meta-population, with a shared history that arose before the "migration" of Aurignacian groups into the Levant, and which defined them as "strangers" to the local Ahmarian groups of the eastern Mediterranean coast. Thus, the

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[3] The Ahmarian differs from the Aurignacian mainly in its characteristic flint tools and the near absence of bone and antler artifacts. It is dated to 46,000–30,000 years and accordingly is contemporaneous with the Levantine Aurignacian (Alex et al., 2017; Goring-Morris and Belfer-Cohen, 2018).

differentiation was not necessarily constrained or dictated by geographic distance. For the Levantine Aurignacian, "otherness" and "strangeness" seem to have been first and foremost constructs of social cognition.

Craft Specialization

We hypothesized (see above) that encounters with strangers should become more apparent in the archaeological record of later periods. We also suggested that their presence can be detected through identification of the products of expert artisans bringing with them knowledge that is new to the local groups.

Although expert lithic knappers may have existed in the Levant as early as the Acheulian, it is of note that their activities are understood as those of local artisans acting within the context of a (sometimes large) residential group (Herzlinger and Goren-Inbar, 2019) of kin (in the extended sense of Bird et al., 2019). Comparable evidence is lacking for most of the Levantine Paleolithic record (possibly due to research/preservation constraints), yet the presence of expert knappers has been recognized in other Paleolithic records, such as the UP Magdalenian culture (ca. 15,000 years ago), in Etiolles, France (Pigeot, 1990 and references therein). There, too, expert knapping occurred within a residential context, and experts are regarded as models for novice knappers.

The context of activities of expert knappers in the Levant seems to have changed in the Pre-Pottery Neolithic B (ca. 10,500–8,400 years ago), possibly as part of the Neolithization processes. The "naviform" mode of flaking stone, designed for the production of long and thin blades, was a pan-Levantine phenomenon (Bar-Yosef and Belfer-Cohen, 1989). Naviform products (arrowheads and sickle blades) expertly produced on non-local raw material, were found together with items sharing the same regional conceptual knowledge yet crudely knapped on local raw material (Barzilai and Goring-Morris, 2007; Khalaily et al., 2007, 2013; Barzilai, 2010; Mitki, 2015). A common explanation of this phenomenon is that the well-made items were introduced into the local communities from outside the region. We maintain that those were produced by expert knappers rather than traded, because of the presence at the sites of production debris besides the finished products (*ibid.*). The material cultural record shows that naviform technology first emerged and evolved in the northern Levant (e.g., current-day central and eastern Turkey, northern Syria), and that its craftsmanship in the north was overall more refined than in the southern Levant. We therefore posit that, heralding from the northern Levant, the expert knappers of naviform items would be perceived as "strangers" by the local communities.

DISCUSSION

Chimpanzees and humans both appear to harbor concepts of "strangers," which may be attributed to a shared evolutionary origin. The encounters of chimpanzee groups with "strangers" are rare, and were reported rather sparsely (e.g., Goodall, 2010; Wilson et al., 2014), because the spatial packing of chimpanzee groups on the landscape typically does not bring groups from different breeding networks into contact. Based on current evidence (which is incomplete for Pleistocene hominins due to the vagaries of time), in human society this SC construct has changed from that of the chimps (and presumably, an early ancestor) during the course of the Pleistocene. We identify the main changes in that the notion of "strangers" is enacted upon constantly in the context of large social networks, and in that it is fluid and transient.

Nearly all researchers agree that hominins, unlike perhaps other species, have found cognitive and social scaffoldings that enable them to operate within very large groups, cross-culturally. It is also clear that at some point in human cultural and social evolution, one's recognition of "group size" shifted from census numbers to a social perception. Notwithstanding any biological limitations on group size, humans acquired a cognitive flexibility that enabled them to first, enlarge the biological and social perception of kin and, secondly, to categorize their social world as one of stable ("kin"/"classificatory kin"/"others") and transient relationships ("strangers"). The latter could be remodeled contextually (i.e., politically, economically or culturally) according to shifting circumstances. Already Isaac (1972) wrote that once culture became more complex and comprehensive and social rules became more structured, it was more likely that internal isolating mechanisms would develop. Gilman (1984) specifically related to shifting circumstances when explaining the difference between the MP vs. UP social interactions. "Thus, as technique improved, relations between groups would become more problematical. [In the earlier periods] the give-and-take of mutual aid would have been so essential that it would have known no social boundaries..." (Gilman, 1984:122). In contrast, in the cultural world of the UP, improved technology led to higher group densities, such that more neighbors became available yet there were fewer occasions on which help from neighboring groups would be required to mitigate environmental risks. "The clear solution to this shift in the balance of a group's interests would be to restrict the scope of its alliances." (*ibid.*). Similar to Stiner and Kuhn (2006), we interpret the UP pattern to suggest higher degrees of connectivity between groups belonging to the same cultural environment, yet we propose that such connectivity was structured differentially across geographic space, with "strangers" located more distally to a given group than were "others." We argue that these large UP groups could not have formed without the emergence of the SC construct of "strangers."

Furthermore, the archaeological evidence allows us to identify earlier-than-expected trends in the emergence of the social cognitive constructs related to inter-personal/intra-group and inter-group behaviors. There is indirect evidence that large social groupings, with their implied categorization of social relationships, emerged earlier than the UP, thus our null hypothesis must be rejected.

We have focused our archaeological discussion on Levantine case studies, using information from lithic raw material, bone tools and personal ornaments. When contextualized against the broader archaeological records of the respective periods outside of the Levant, archaeological data provide insights of similar social cognitive constructs. For example, larger transport distances of raw material entailed, almost by default, awareness and recognition of "strangers." Long transport distances of obsidian in eastern Africa (>200 km and sometimes >300 km; Blegen, 2017; Merrick et al., 1994; Negash and Shackley, 2006) are reported from the early Middle Stone Age (MSA; ca. 320,000–50/40,000 years ago) onward. These data could be interpreted to reflect large home ranges of "others" acting within a social/cultural group, interacting directly at the obsidian sources. More likely, this pattern should be attributed to indirect procurement (e.g., Merrick et al., 1994; Tryon and Faith, 2013) through the agency of "strangers." Indeed, it has been argued that this very pattern reflects the increase in spatial extent of the social networks, as is the case with modern hunter-gatherers (Pearce, 2014; Pearce and Moutsiou, 2014). Similar behaviors may explain the distances of obsidian transport in the Caucasus (see discussion in Doronicheva and Shackley, 2014), which in some cases were >500 km during the late MP and the UP (Frahm et al., 2019). The late MP in Eurasia may be the first time when "strangers" become an element of the social structure, within networks of partial connectivity greatly contributing to the growth and evolution of human culture at large (Derex and Boyd, 2016; Premo, 2016; Derex et al., 2018). In fact, this may be the continuation of a trend that had started in the Middle Pleistocene (e.g., Rolland, 2004; Kuhn and Stiner, 2019) and gradually increased through time, as indicated by the Eurasian UP record in general (Stiner and Kuhn, 2006), and the Levant specifically (see above).

A known phenomenon in the south Levant, of sites dating to Late UP [Epipalaeolithic] and Neolithic times, is that of obsidian sourced to central and northern Anatolia. This is parsimoniously explained as evidence of down-the-line trade or exchange (see Ammerman, 1979 for a case study outside the Levant) involving "others" and/or "strangers," which grew in scope with the process of Neolithization. Indeed, the evidence for the activities of non-local expert knappers in south Levantine Early Neolithic villages corroborates such interpretations. In fact, this may be the culmination of a trend that had started ca. 400,000 years ago, in the late Middle Pleistocene (e.g., Kuhn and Stiner, 2019) and gradually increased through time, as indicated by the Eurasian UP record in general (Stiner and Kuhn, 2006; and see above).

As we understand it, the trend is consistent with Isaac (1972) and Gilman (1984) insights that as economy and technology became more complex, it required constant evaluation of social cognitive rules and their ongoing restructuring within the respective cultural contexts. The separation between "us" and "others" *vis-a-vis* "strangers" would be instrumental in alleviating "scalar stress" (as defined by Johnson, 1982) within a large group. The breaking down of larger and growing social units into smaller, conceptually "manageable" ones, would require the creation of social stereotypes that one could allude to (see also Cohen, 1985). This is a process that has been observed in historical and extant societies and apparently is still ongoing. A historical example is the ancient Greek worldview, by which a social universe was divided almost by default into two: "us" (and all related "others"), meaning familiar, Greek-speaking individuals/political entities; and the rest of the world populations, "strangers," i.e., unfamiliar individuals/political entities that did not speak the language, all of them stereotyped as "Barbarians." In fact, to this day group identity creates cognitive social and economic biases and stereotypes that affect venues of modern life (e.g., Cacault and Grieder, 2019). In this sense, SC constructs that have emerged in deep prehistoric times affect many aspects of our modern lives, in an ongoing process of self-domestication.

AUTHOR CONTRIBUTIONS

Both authors perceived and wrote the manuscript.

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REVIEW
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Why Care: Complex Evolutionary History of Human Healthcare Networks

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One of the striking features of human social complexity is that we provide care to sick and contagious individuals, rather than avoiding them. Care-giving is a powerful strategy of disease control in human populations today; however, we are not the only species which provides care for the sick. Widespread reports occurring in distantly related species like cetaceans and insects suggest that the building blocks of care for the sick are older than the human lineage itself. This raises the question of what evolutionary processes drive the evolution of such care in animals, including humans. I synthesize data from the literature to evaluate the diversity of care-giving behaviors and conclude that across the animal kingdom there appear to be two distinct types of care-behaviors, both with separate evolutionary histories: (1) social care behaviors benefitting a sick individual by promoting healing and recovery and (2) community health behaviors that control pathogens in the environment and reduce transmission within the population. By synthesizing literature from psychology, anthropology, and biology, I develop a novel hypothesis (Hominin Pathogen Control Hypothesis) to explain how these two distinct sets of behaviors evolved independently then merged in the human lineage. The hypothesis suggests that social care evolved in association with offspring care systems whereas community health behaviors evolved as a type of niche construction. These two types of behaviors merged in humans to produce complex, multi-level healthcare networks in humans. Moreover, each type of care increases selection for the other, generating feedback loops that selected for increasing healthcare behaviors over time. Interestingly, domestication processes may have contributed to both social care and community health aspects of this process.

Keywords: care-giving, illness, disease, social cognition, self-domestication, human evolution, niche construction, eusocial

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WHAT ARE HEALTHCARE BEHAVIORS?

Human healthcare, including biomedical care, has enabled our species to exert an unprecedented amount of control over the pathogens which affect our species (Ferguson et al., 2003; Kessler et al., 2017, 2018). We synthesize medications, track the evolution and outbreak of novel diseases (Jones et al., 2008), and have even eradicated pathogens using vaccines (Ferguson et al., 2003). While these activities are clearly unique to our species, once healthcare behaviors are separated from medical technologies, we see intriguing continuities and convergences in healthcare behaviors across the animal kingdom. It is these patterns of care-giving behaviors that offer the opportunity to examine the underlying evolutionary processes driving them, including when, how, and why, care-giving in health contexts got scaled up in our species.

Here, I define healthcare behaviors as a group of behaviors which can control diseases. Because the outcomes of individual infections influence transmission dynamics within a community, this definition includes both behaviors that can control disease progression within infected individuals and behaviors that can control transmission through communities.

This definition means that healthcare behaviors can be paradoxical. Some behaviors promote recovery when given to diseased individuals, i.e., provisioning or guarding animals that might not survive otherwise, whereas other behaviors are harmful to diseased individuals, but protective for the community. For example, termites cannibalizing nest-mates which have been infected with a fungal pathogen do not benefit the infected individuals, but if the cannibalization deactivates the fungal propagules as they pass through the cannibalizer's digestive tract, it does protect other nest-mates from exposure (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). In addition, some healthcare behaviors, like grooming, are widespread across taxa (Lehmann et al., 2007; Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Bush and Clayton, 2018), while others are restricted to only a few relevant species. For example, lifting a sick conspecific to breathe at the surface of a body of water (Bearzi et al., 2018) is only necessary in aquatic mammals. Understanding the complex transmission dynamics produced by different types of behaviors and their distribution across species is central to understanding how healthcare behaviors evolve.

In the next section, I examine healthcare behaviors observed in non-human animals while paying particular attention to who the beneficiary is (a specific individual vs. the community in general) and the implications of the behavior for disease transmission. I use *healthcare behaviors* as an umbrella term which encompasses both healthcare behaviors directed toward an individual [*social care*, hereafter, also referred to as conspecific care or social support in the anthropological literature (DeGusta, 2003; Hublin, 2009; Turner et al., 2014)] and healthcare behaviors which benefit the community (*community health behaviors*, hereafter, to reflect the division between medical care for patients and public health in humans today). I deal with these two types of healthcare behaviors separately because a central goal of this paper is to further our understanding of how these two processes may have interacted during human evolution. Notably, these definitions exclude self-directed care and other forms of care, like parental care, which are not specific to health contexts.

Because animals (including humans) may have difficulty determining when a conspecific has an infectious vs. non-infectious condition (injury, disability, non-contagious diseases, etc.), social care for individuals with infectious and non-infectious conditions are unlikely to have evolved independently. As it is more costly to provide care to infectious individuals (one might contract the disease), if animals are unable to accurately distinguish infectious from non-infectious individuals, yet still provide care, non-infectious individuals will lower the costs of providing care when *averaged over many care-giving events*. Over an evolutionary scale, this may be relevant to understanding how social care could be perpetuated in populations, despite the risks that they pose for the carer. Therefore, I include responses to non-contagious conditions as well. Similarly, I also include responses to dead individuals because (1) care behaviors may start before death and continue afterward (Anderson et al., 2010; Bearzi et al., 2018) and (2) corpses are potential sources of pathogens (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Cremer et al., 2018; Porter et al., 2019).

To my knowledge, this is the first review which integrates the biological literature (animal behavior, citations below) with the psychological and anthropological literature [e.g., compassion (Gilbert, 2017; Seppälä et al., 2017) and attachment theory (Fogel and Melson, 1986; Preston, 2013; Cassidy and Shaver, 2016), fossil evidence of social care during human evolution (Dettwyler, 1991; Lebel et al., 2001; DeGusta, 2003; Hublin, 2009; Spikins, 2015; Spikins et al., 2018, 2019)] to produce a new hypothesis explaining the integration of social care and community health behaviors. These healthcare behaviors are part of the behavioral immune system (Schaller and Park, 2011) but focus on a specific subset of the behavioral immune system – the contexts in which individuals suppress disgust, fear, and avoidance responses to engage in behaviors that benefit others (Peng et al., 2013; Preston, 2013). While this review aims to provide a broad overview, I pay particular attention to primates for their evolutionary relationship to humans, cetaceans, and birds for their convergences with humans in cognition, and eusocial insects (Hymenoptera: ants, bees, wasps, and Isoptera: termites) for their convergences with humans without complex cognition. While the selection of species may appear an unsystematic collection of anecdotes, this is largely a reflection of the discipline at present; these are the taxa which have received the most attention, first as anecdotal reports by field researchers and then, with taxa specific reviews (e.g., Bearzi et al., 2018; Bush and Clayton, 2018; Reggente et al., 2018; Watson and Matsuzawa, 2018). This has had the unintended effect of making the discipline fairly "siloed." One of the goals of this paper is to look across taxa and behaviors to identify patterns and start building a broader theoretical framework for understanding the evolution of healthcare behaviors. I hope that this will lay the foundation for future work which can test this theoretical framework.

SOCIAL CARE: BEHAVIORS BENEFITTING AN INFECTED INDIVIDUAL

Grooming

Allogrooming is widespread across the animal kingdom [i.e., primates (Lehmann et al., 2007), birds (Bush and Clayton, 2018), ungulates (Hart and Hart, 2018), and insects (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013)]. This includes removing ectoparasites with hands (Lehmann et al., 2007), bills (Bush and Clayton, 2018), teeth (Hart and Hart, 2018), or mouthparts (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). Although many species appear to tolerate some ectoparasites (Hart, 2011), they may also be vectors of other diseases (Sadanandane et al., 2018), making their removal beneficial for both the parasitized individual and the wider social group. Analyses of grooming patterns have shown that for many species, grooming is a key mechanism for establishing and maintaining relationships with kin, allies, or mates and maintaining group cohesion (Lehmann et al., 2007). However, it also serves important hygienic functions (Hart and Hart, 2018). While most animals can self-groom, social grooming is particularly important for areas of the body which the animal cannot reach (Hart and Hart, 2018). For example, allopreening occurs in at least 50 families of birds and controls parasites on the head and neck areas that the bird itself can't reach (Bush and Clayton, 2018). Fungal infections are a key driver of allogrooming in many eusocial insects (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Cremer et al., 2018; Liu et al., 2019). If the infectious spores aren't removed before they penetrate the cuticle, they cause an infection which is fatal to the infected individual and dangerous to other nest-mates (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Cremer et al., 2018; Liu et al., 2019). These examples demonstrate the importance of allogrooming to both in the infected individual and to the broader community (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Cremer et al., 2018; Liu et al., 2019).

Another component of grooming is wound-cleaning, which may include removing debris and licking wounds, behavior which manually washes debris out of a wound and applies saliva to it (Hart, 2011). Saliva has antibacterial properties which may promote healing (Hart and Powell, 1990; Hart and Hart, 2018). For example, termite-hunting ants (*Megaponera analis*), which incur high levels of injuries when hunting, carry wounded nest-mates back to the nest and provide care to the injuries (Frank et al., 2018). Ants with one or two bitten off legs are carried back and the wounds are licked by the other ants (Frank et al., 2018). Recovery of ants provided with such care is 80%, compared to 10% in ants who received no care (Frank et al., 2018). Ants who have healed after having extremities bitten off are able to return to hunting, potentially explaining why this species evolved this form of social care (Frank et al., 2018). Interestingly, ants who had five legs removed are not carried back to the nest, but this appears to be regulated by the injured ant itself, in that it is unable to position itself correctly to be carried back (Frank et al., 2018).

The extent to which grooming may increase transmission through exposing the groomer is unknown and likely depends on the transmissibility of the parasite and how intimately the groomer interacts with the infected individual. However, because grooming often occurs along established social (often kinship) networks, it is possible that because these individuals are already likely to be in close proximity that grooming does not significantly elevate the risk that already exists (Griffin and Nunn, 2012).

Social Anointing

Self-anointing occurs when individuals rub substances, or even ants, on their bodies (Bush and Clayton, 2018). Social anointing occurs when individuals apply it to others (Bowler et al., 2015). These behaviors are common in eusocial insects which secrete antifungal and antibacterial substances which they apply to nest-mates through allogrooming (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Liu et al., 2019). In eusocial Hymenoptera, these substances are secreted by Dufour's, mandibular, venom, and metapleural glands and in Isoptera by sternal glands, head glands, and rectal fluids (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). Many insect species also secrete antimicrobial substances and apply them to their eggs or larvae in the nest (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013).

While self-anointing, including with ants, occurs frequently in birds (Bush and Clayton, 2018), to my knowledge, only one bird species has been observed socially anointing. The crested auklet (*Aethia cristatella*), a colonial species of seabird, anoints prospective mates with a substance released from its specialized wick-like feathers (Douglas, 2008). The volatile compounds from the secretions paralyze and kill lice (Douglas, 2013).

Within primates, social anointing appears to be restricted to a few new world monkey taxa: the untufted capuchins (Alfaro et al., 2012) (*Cebus*), tufted capuchins (Alfaro et al., 2012) (*Sapajus*), and owl monkeys (Jefferson et al., 2014) (*Aotus*). Monkeys have been observed socially anointing using a variety of strongly smelling plants, mud, or insects which can be crushed into the fur or stimulated into secreting compounds (millipedes, stink bugs, ants) (Alfaro et al., 2012). Interestingly, in general *Cebus* tends to use more plants, while *Sapajus* uses more insects (Alfaro et al., 2012). Most social anointing occurs with group-mates in physical contact, but still directing most (or all) of the rubbing to their own bodies (Alfaro et al., 2012). However, anointing others, particularly infants, has also been observed and, even when most rubbing is self-directed, being in physical contact with others who are anointing helps to distribute the substances more evenly (Alfaro et al., 2012). Analyses of which body parts get covered has shown that self-anointing is focused on areas that are out of sight on the body, while social anointing tends to increase coverage of areas that are hard to reach, suggesting that social anointing does have a hygienic effect (Bowler et al., 2015). One of the leading hypotheses for social-anointing in general is that it is mutual medication (Bowler et al., 2015), which serves to protect individuals against ectoparasites and biting flies, both through individual protection and by reducing the general attractiveness of the group to parasites.

In many mammals, grooming may be performed with the mouth (i.e., tongue, teeth, etc.), meaning that it involves applying saliva to another individual (Hart and Hart, 2018). The extent to which this serves as social anointing is currently unknown, because it's unclear to what extent the saliva protects against pathogens when applied to fur or an uninjured body surface. This would be an interesting area for future work.

Guarding

Remaining near or guarding (repelling others) can protect a vulnerable individual from attacks by conspecifics and predators. It has been observed in chimpanzees [*Pan troglodytes* (Anderson, 2016; Watts, 2019)], gorillas [*Gorilla beringei* (Porter et al., 2019; Watts, 2019)], marmosets [*Callithrix jacchus* (Bezerra et al., 2014)], ring-tailed lemurs [*Lemur catta* (Nakamichi et al., 1996)], snub-nosed monkeys [*Rhinopithecus* *roxellana* (Yang et al., 2016)], elephants [*Loxodonta africana* (Douglas-Hamilton et al., 2006)], giraffe [*Giraffa camelopardalis* (Bercovitch, 2013; Strauss and Muller, 2013)], peccaries [*Pecari tajacu* (de Kort et al., 2018)], dingos [*Canis dingo* (Appleby et al., 2013)], mongooses [*Helogale parvula* (Rasa, 1983)], and pinnipeds (Reggente et al., 2018). This behavior includes waiting for a conspecific that cannot keep up, standing over a conspecific that is unable to move, or chasing away conspecifics and predators (citations above). In general, guarding is frequently given to kin or to past or future mates [marmosets (Bezerra et al., 2014), gorillas (Porter et al., 2019), and snub-nosed monkeys (Yang et al., 2016)]. For species at a high risk of predation or intra-species aggression, guarding is likely to be valuable. This investment is likely to be costly for the carer, as it may require the carer to forgo foraging opportunities, incur higher predation risks when separated from the social group and standing near a vulnerable individual who may attract predators, or engage in aggressive encounters when driving away others (Bercovitch, 2013; Strauss and Muller, 2013). The extent to which the carer incurs a risk of disease transmission will depend on the proximity of the carer to the contagious individual and how transmissible the pathogen is (Porter et al., 2019). When the individual is infectious, driving away others may also decrease exposure within the population (Hart and Hart, 2018).

Provisioning

Provisioning wounded or ill group members has been observed in wild mongooses [*H. parvula* (Rasa, 1983)], lions [*Panthera leo* (Hart, 2011)], foxes (Hart, 2011), and giant otters [*Pteronura brasiliensis* (Davenport, 2010)]. This may take the form of tolerating a food theft or providing food to a begging individual (Davenport, 2010). Interestingly, these species may share food and/or cooperatively raise young. For cooperatively breeding species, such care may be a form of kin selection (Rasa, 1983). If the injured/sick individual is related to the carer and may help rear future offspring to whom the carer will also be related, providing care is an investment in both the injured/sick individual and in the future offspring (Rasa, 1983). Provisioning is likely to be particularly valuable to individuals undergoing a long period of injury or illness that prevents obtaining their own food (Sugiyama, 2004; Davenport, 2010). The costs to the carer will likely depend on whether the carer is still able to obtain adequate nutrition. The extent to which the carer incurs a risk of disease transmission will depend on the proximity of the carer to the contagious individual and how transmissible the pathogen is.

Carrying/Supporting

Carrying and/or supporting a sick or injured individual (hereafter, carrying) has been observed in multiple species (e.g., Appleby et al., 2013; Reggente et al., 2018), but received particular attention in two taxa: non-human primates (Watson and Matsuzawa, 2018) and cetaceans (Bearzi et al., 2018). In primates mothers (and others) may carrying infants long after death (Watson and Matsuzawa, 2018), even as the corpses putrefy and decay (Biro et al., 2010). Corpse carrying has been observed in chimpanzees, bonobos (*P. paniscus*), orangutans (*Pongo abelii*), gorillas, multiple species of macaques (*Macaca* ssp.), geladas (*Theropithecus gelada*), langurs (*Rhinopithecus bieti*), snub nosed monkeys and capuchins (Watson and Matsuzawa, 2018). One wild chimpanzee mother was observed carrying the body of her infant for over 2 months after it died of a respiratory illness (Biro et al., 2010). During that time, the body swelled and mummified (Biro et al., 2010). For primate and non-primate species that do not carry, physical constraints, like body size, may make it impossible (Nakamichi et al., 1996). For example, ringtail lemur mothers have been observed attempting to carrying older infants that were unable to move on their own, but too big for the mother carry (Nakamichi et al., 1996).

However, within species that do carry dead infants, we also do not yet have a good understanding of the variation that we observe in carrying behavior (Watson and Matsuzawa, 2018). We do not yet understand why, even within the same population or social group, some females carry and others do not (Watson and Matsuzawa, 2018). Similarly, we also do not understand why, even within the same female, she may carry one of her infants when it dies but not another (Watson and Matsuzawa, 2018). She may even engage in both carrying behavior and cannibalizing the corpse (Watson and Matsuzawa, 2018). The behavior appears to be complex and maybe influenced by the age and weight of the infant, how the infant died, the social rank and experience of the mother, and the climate (Watson and Matsuzawa, 2018).

The other taxa in which carrying behavior has received particular attention are the aquatic mammals – species in which carrying and lifting an animal to the surface to breathe can be life-saving (Bearzi et al., 2018). In cetaceans attending to a corpse has been observed to continue for up to a week (Bearzi et al., 2018). In an analysis of reports of attentiveness to dead conspecifics across cetaceans, 20 of 88 living species were found to engage in it ($N = 78$ records) (Bearzi et al., 2018). However, dolphins accounted for 92% of these records (Bearzi et al., 2018). Of the cases where the sexes of the potential carers were known ($N = 28$), 75% included adult females and an immature who may have been the females' offspring (Bearzi et al., 2018). While this appears to suggest that maternal bonds may be frequent conduits for care-giving in the intelligent and socially complex dolphins, the authors point out that there are several factors that make it difficult to generalize with confidence (Bearzi et al., 2018). They include unequal amounts of research effort across species, differences in dive behavior across species influencing the likelihood of observing a species at the surface, and differences in corpse buoyancy across species (more likely in species with thick blubber) and within species (influenced by gaseous build up during decomposition and possibly by age/size) (Bearzi et al., 2018). These factors may make the sample biased (Bearzi et al., 2018).

Thermoregulatory Assistance

Thermoregulatory assistance has not received a great deal of attention across species, but is an interesting avenue for future work. Honeybees (*Apis mellifera*) produce a behavioral fever in the brood-comb when larvae become infected with the heat-sensitive fungus *Ascosphaera apis* (Starks et al., 2000). The bees isometrically contract their thoracic muscles to raise their thoracic temperature and put them near the brood cells (Wilson-Rich et al., 2009). A study with an experimental infection showed that infected colonies raised the brood-comb temperature above the pre-infection temperature (Starks et al., 2000). No such increase was observed in the control colony (Starks et al., 2000). While other species, particularly birds and reptiles, may control pathogens by sunning (Bush and Clayton, 2018), those behaviors are generally self-directed, rather than providing care to others. Researchers working with species that huddle or engage in torpor, may want to look for instances of inducing behavioral fevers in conspecifics who are ill.

COMMUNITY HEALTH BEHAVIORS

Nest Sanitation

Nest sanitation behaviors like removing waste and replacing contaminated/infested nest materials are common in birds (Ibáñez-Álamo et al., 2014; Ibanez-Alamo et al., 2016; Diego Ibanez-Alamo et al., 2017; Bush and Clayton, 2018) and eusocial insects (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). For example, house wrens (*Troglodytes aedon*) are thought to reduce the abundance of mites (*Dermanyssus*) by removing old nesting material and great tits (*Parus major*), blue tits (*Cyanistes caeruleus*), and pied fly catchers (*Ficedula hypoleuca*) show more nest sanitation behaviors when ectoparasites are present than when they are not (Bush and Clayton, 2018). Phylogenetic analyses of parental nest sanitation showed that parental removal of nestling feces drove the evolution of fecal sacs (a mucus covering that encloses nestling feces and accompanying bacteria) (Ibáñez-Álamo et al., 2014; Diego Ibanez-Alamo et al., 2017). Moreover, experimental studies showed that breaking the fecal sacs resulted in nestlings with more ectoparasites and lower probabilities of survival (Azcarate-Garcia et al., 2019), suggesting that feces removal is beneficial for nestling health.

Eusocial insects also show nest sanitation behaviors, particularly for waste removal (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). Honeybees defecate when flying away from the nest, paper wasps which build nests that hang from trees drop larval meconial outside the nests, and other taxa (ants, aphids, social mites, and others) defecate in refuse dumps located away from the nest, at the border of the nest, or in special chambers within the nest (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). These behaviors reduce the risk of nests transmitting infections to nest-mates (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). A promising area of future research would be to conduct comparative work on other nest-living, burrowing, and den-living taxa.

Interesting comparisons in non-nest living species also include the evolution of latrine behaviors, in which animals defecate in restricted areas. There are extensive literatures on animal latrines focusing on intraspecific studies of the communicative functions (e.g., Irwin et al., 2004; Barja and List, 2006; Wronski et al., 2006; Jordan et al., 2007; Ruibal et al., 2010; Droescher and Kappeler, 2014; Rodgers et al., 2015; Barocas et al., 2016; Eppley et al., 2016; King et al., 2017) and seed dispersal (Feeley, 2005; Pouvelle et al., 2009; Dos Santos Neves et al., 2010; Gonzalez-Zamora et al., 2012; Zarate et al., 2019), but the distribution of defecation behaviors across species, their implications for concentrations of pathogens across the landscape (Nunn and Dokey, 2006; Nunn et al., 2011, 2014; Numberger et al., 2019), and how this may drive the evolution of latrine behaviors is not fully understood.

Nest Fumigation

This behavior shows interesting convergences between birds and insects. Several bird species, most commonly cavity nesting birds, incorporate fresh aromatic herbs into their nests (Scott-Baumann and Morgan, 2015). The leading, non-mutually exclusive hypotheses are that it evolved through sexual selection (i.e., male starlings bringing herbs to nests as mating effort), nest protection hypothesis (herbs decrease parasites or pathogens, i.e., lice, mites, fleas, blowflies, midges, blackflies, or bacterial colony numbers, richness or diversity in nests), or the drug hypothesis (herbs do not reduce parasite numbers, but improve the health of the chicks directly, possibly by potentiating their immune systems) (Scott-Baumann and Morgan, 2015). Overall the evidence for these three hypotheses is suggestive of complex evolutionary causes, but not conclusively understood (Scott-Baumann and Morgan, 2015). The evidence for sexual selection is strongest in starlings where males bring the herbs until the females begin laying, and (in spotless starlings, *Sturnus unicolor*) the females may even remove the herbs as they are brought (Scott-Baumann and Morgan, 2015), suggesting that it is not left in the nest to benefit future offspring. In blue tits females bring the herbs during the hatchling period (Scott-Baumann and Morgan, 2015). Experimental manipulations of herbs in nests produced evidence suggesting that herbs decrease nest parasites/bacteria or increases in chick health/nest success, but usually did not produce simultaneous evidence of both (Scott-Baumann and Morgan, 2015). Similarly, house sparrows (*Passer domesticus*) and house finches (*Carpodacus mexicanus*) incorporate fibers of cigarette buts into their nests, with nests with a high density of them having lower mite densities (Bush and Clayton, 2018). Although less well studied, similar studies have linked green vegetation in songbirds with lower botfly infestations (*Philonis* spp.), pine materials with less blowfly larvae (*Protocalliphora*) in eagle nests (*Hieraaetus fasciatus*), and yarrow (*Achillea millefolium*) with fewer fleas in tree swallow nests (*Tachycineta bicolor*) (Bush and Clayton, 2018).

Similarly, insects also incorporate protective substances into their nests. For example, honeybees build their combs out of a mixture of resins that they have gathered and antibiotic substances in their saliva (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). They also coat the walls of their nests with bodily secretions containing antimicrobials (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). Termites construct their nests using soil and feces, which contain antimicrobial and antifungal substances (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). Ants also secrete antimicrobial substances which they distribute on themselves, their nest-mates via allogrooming, and the nest (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013).

Nest fumigation with volatile compounds has been suggested to occur in insects Formosan subterranean termites [*Coptotermes formosanus* (Chen et al., 1998)] and red imported fire ants, [*Solenopsis invicta* (Wang et al., 2015)]. Nest fumigation in mammals has received less research, but there is some evidence for convergent evolution. The dusky-footed wood rat (*Neotoma fuscipes*) has also been documented to use bay leaves (*Umbellularia californica*), similarly to birds, to control fleas in the nest (Hemmes et al., 2002). Similar hypotheses have been suggested for the cedar, *Thuja occidentalis*, that flying squirrels, *Glaucomys sabrinus*, and red squirrels, *Tamiasciurus hudsonicus*, use to construct their nests (Patterson et al., 2007). Additional research into the choice of nesting materials in small mammals would be particularly informative in understanding the evolution of fumigation behaviors. Overall, the diversity of ways in which anti-pathogenic substances are incorporated into nests across taxa suggest that there are strong selective pressures for reducing pathogens in nests.

Undertaking: Disposal of the Dead (Burial, Removal, Cannibalism)

Corpse management appears to be relatively unusual outside of humans and insects. Rodents will bury corpses in response to olfactory cues emitted through decomposition (Pinel et al., 1981) and in one case, a wolf mother (*Canis lupus*) was inferred to have buried her dead pups (Boyd et al., 1993). The researchers found locations where pups appeared to have been buried, then subsequently dug up and taken away by scavengers (Boyd et al., 1993). The authors speculated that the mother may have buried the first few pups after they died while still caring for the remaining pups until they too died (Boyd et al., 1993). The cause of death was thought to be canine distemper virus or canine parvovirus (Boyd et al., 1993).

Eusocial insects show an intriguing diversity of corpse management strategies, including combinations of necrophoresis (transporting the dead), necrophagy/cannibalism (eating dead, injured, or diseased individuals), burial, or necrophobia (avoidance) (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Sun and Zhou, 2013). There are two broad combinations which vary by taxa (Hymenoptera and Isoptera) (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). Eusocial Hymenoptera: In these taxa, the primary strategy is necrophoresis, but the brood may be eaten (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). Corpses, refuse piles, and locations where corpses were generally avoided (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). Burial is not a primary strategy, but does occur (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). In Isoptera necrophagy is the main strategy, but corpses are also buried (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). Corpses and burial locations are generally avoided (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). Because corpses are sources of disease, disposing of them is both an important way of reducing pathogens in the nest and a dangerous activity for the individuals dealing with the corpses (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013).

Undertakers: Divisions of Labor

Eusocial insects are well known for their complex divisions of labor within the colony, and in some taxa, this includes undertaking and hygienic behaviors (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Stroeymeyt et al., 2014). In the eusocial Hymenoptera, the main strategy of corpse management is corpse removal, and this task is performed primarily by subcastes of workers who specialize in these tasks (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Sun and Zhou, 2013). These individuals are frequently older, with genetic, hormonal, and neurological differences from others which may predispose them to being sensitive to the chemical signals of death and working without a circadian rhythm enabling quick removal of corpses (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). This specialization, particularly by age, means that younger individuals tend to work inside the nest and tend to the brood, while older individuals engage in riskier tasks outside the nest which bring them in to contact with additional pathogens (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Stroeymeyt et al., 2014). In colonies of fungus growing ants, there is a strict division of labor among workers who forage and workers who transport waste to garbage dumps (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Stroeymeyt et al., 2014). The dump workers are older ants who are actively rejected by other nest-mates if they try to leave the dump, thus enforcing strict spatial and social barriers to pathogen transmission (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Stroeymeyt et al., 2014).

In contrast, Isoptera do not have a subcaste of workers which specializes in corpse disposal (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Sun and Zhou, 2013). Instead, corpses are generally eaten or buried and burials are generally performed by groups of workers (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). While termite workers may not specialize in undertaking, in some species soldiers do not participate in burials (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). While I have discussed the broad patterns that we observe, these behaviors are complex and do vary between species within the Hymenoptera and Isoptera (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). Engaging in these risky behaviors like waste and corpse removal is likely to be maintained by kin selection (Cremer et al., 2007; Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Sun and Zhou, 2013; Stroeymeyt et al., 2014; Shakhar, 2019). In eusocial insects, the workers are non-reproductive, but highly related to the others in the colony, thus performing tasks that benefit the colony as whole, including the reproductives, is a way for them to pass a portion of their genes in to future generations (Cremer et al., 2007; Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Sun and Zhou, 2013; Stroeymeyt et al., 2014; Shakhar, 2019).

THE HOMININ PATHOGEN CONTROL HYPOTHESIS

When we look across animals, the two types of healthcare behaviors, social care and community heath behaviors, produce a mosaic pattern across species. This section of the paper proposes a novel, testable hypothesis (Hominin Pathogen Control Hypothesis, **Figure 1**) which explains the evolution and

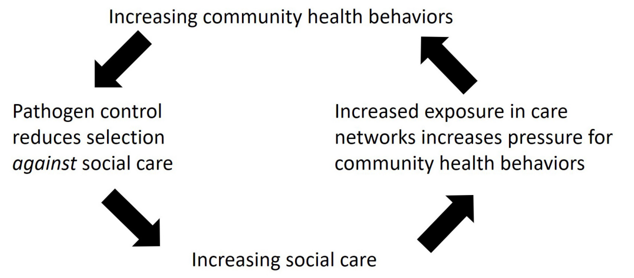

FIGURE 1 | Schematic diagram of the Hominin Pathogen Control Hypothesis. The arrows show the hypothesized selection pressures predicted to increase social care and community health behaviors in hominins during human evolution.

integration of these two types of healthcare behaviors in humans, based on the patterns we see across animals. The hypothesis suggests that social care evolved in association with offspring care systems and social cognition pathways in the brain (Preston, 2013). Thus, many of the social care behaviors that are common between humans and animals, i.e., guarding sick individuals, are likely shared with our most recent common ancestors. In contrast, the evolutionary history of community health behaviors appears to be different. Using niche construction theory (Laland et al., 2016, 2017) as a framework for understanding community health behaviors (Hurtado, personal communication, 2018) enables these behaviors to be understood as techniques for controlling pathogens in the constructed environment, e.g., within nests. This interpretation suggests that many of the community health behaviors common between humans and animals, i.e., birds or insects, are derived behaviors that evolved through convergent evolution.

Finally, one of the striking characteristics of human healthcare behaviors is how frequent and widespread they are. The Hominin Pathogen Control Hypothesis predicts that feedback loops created by social care and community health behaviors created increasing pressure on each type of behavior (**Figure 1**). Social care, when given to sick and contagious individuals, is predicted to actually *increase* the risk of disease transmission to susceptible carers, thereby putting the broader community at risk (Kessler et al., 2018). This is predicted to create selection for community health behaviors that reduce transmission (e.g., sanitation, fumigation, disposal of the dead), thereby *reducing* selection *against* social care and allowing it to become more frequent in the population. Overall, this produces a feedback loop that selects for increasing social care and community health behaviors over time (**Figure 1**).

Social Care Uses Parent–Offspring Care and Social Cognition Pathways

Many of the behaviors categorized as social care are behaviors that are commonly given from parents to vulnerable offspring, e.g., provisioning and carrying. Moreover, carers are frequently, although not always, mothers. And indeed, one of the leading hypotheses explaining behaviors like continuing to carry around corpses long after they have started to decompose, providing strong visual, olfactory, behavioral, and tactile cues of death, is that it maybe a by-product of the maternal bond (Biro et al., 2010; Bearzi et al., 2018; Watson and Matsuzawa, 2018).

Social care, when given to a genetic relative, may increase the carer's inclusive fitness if the recipient recovers and reproduces (Kessler et al., 2017, 2018; Shakhar and Shakhar, 2015; Shakhar, 2019). The idea that inclusive fitness may be a key driver of care among relatives is also supported by the frequent appearance of species which tend to show cooperative behaviors [i.e., alliances in primates and cetaceans (Chapais, 1995; Parsons et al., 2003), and cooperative hunting/provisioning of young in some carnivores (Davenport, 2010)].

Potential links between offspring care and social care for the sick have also attracted attention from researchers focused on the proximate mechanisms of compassion (Gilbert, 2017; Seppälä et al., 2017) and attachment (Fogel and Melson, 1986; Cassidy and Shaver, 2016). Preston (2013) unifies ultimate explanations of altruistic responses to distressed or needy individuals with the proximate mechanisms underlying offspring care systems. Altruistic responding is defined as, "as any form of helping that applies when the giver is motivated to assist a specific target after perceiving their distress or need (Preston, 2013, p. 1307)." Social care for the sick fits well within that definition and can be thought of as a subtype of altruistic responding. Preston (2013) roots the mechanisms of altruistic responding in the physiology and neurobiology of offspring care systems, describing the role of oxytocin in reducing avoidance behaviors, dopamine in motivating approach behaviors, and the anterior cingulate cortex and prefrontal cortex in regulating emotion and decision-making processes.

However, while the cues that sick individuals provide may overlap with those of offspring (i.e., inability to forage), they are not the same. This suggests that the process for recognizing when individuals need care requires more than simply activating offspring care behaviors. There is a growing consensus that the process of evaluating the health status of others is an aspect of social cognition (Fisher et al., 2014; Shakhar and Shakhar, 2015; Steinkopf, 2015; Tiokhin, 2016; Kessler et al., 2017; Kavaliers and Choleris, 2018; Steinkopf and de Barra, 2018). The same brain pathways that enable animals to interpret behavioral, olfactory, vocal, or visual cues to discern the identities, motivations, and intentions of others can likely detect health cues such as lethargy or difficulties moving, odor changes due to immune responses, respiratory infections in vocalizations, or fevers and rashes on faces (Fisher et al., 2014; Shakhar and Shakhar, 2015; Steinkopf, 2015; Tiokhin, 2016; Kessler et al., 2017; Kavaliers and Choleris, 2018; Steinkopf and de Barra, 2018). This would suggest that recognizing health cues in others may be a key aspect of social cognition and/or that these pathways may have been co-opted for that use (Fisher et al., 2014; Shakhar and Shakhar, 2015; Steinkopf, 2015; Tiokhin, 2016; Kessler et al., 2017; Kavaliers and Choleris, 2018; Steinkopf and de Barra, 2018).

This is *tentatively* supported by the frequent observations of care in species with greater cognitive abilities and complex social relationships like the cetaceans (Bearzi et al., 2018), primates (Anderson et al., 2010), or carnivores (Davenport, 2010). It may suggest that the aspects of the social cognition which facilitate close relationships may contribute to the development of care-relationships (Fisher et al., 2014; Shakhar and Shakhar, 2015; Steinkopf, 2015; Tiokhin, 2016; Kessler et al., 2017; Kavaliers and Choleris, 2018; Steinkopf and de Barra, 2018). However, this observation must, at present, remain tentative because they are also taxa which have received a great deal of research effort *because of* their reputations for social complexity. There is a need for investigations into understudied species and for researchers to report a *lack of social care* when opportunities were present but no care was given. Turner et al. (2014) is an excellent example of this, reporting that a population of Japanese macaques (*Macaca fuscata*) with a high rate of congenital limb malformations, does not provide care to disabled group members.

Community Health Behaviors: Pathogen Control as a Key Element of Niche Construction

All living organisms modify their environment (Laland et al., 2017). This includes striking behaviors like building webs, nests, or dams, and more subtle environmental changes like plants altering the temperature, moisture level, and composition of the soil around them (Laland et al., 2017). This phenomenon in which organisms modify, or "construct," aspects of their environment is called niche construction (Laland et al., 2017).

Niche construction theory (Laland et al., 2016, 2017) can be used as a framework for understanding how community health behaviors can control pathogens in the constructed environment (Hurtado, personal communication, 2018). As pathogen control techniques, they are part of the species behavioral immune system [psychological and behavioral defenses against disease (Schaller and Park, 2011)] and contribute to the social immunity of the population [collective defenses against disease (Cremer et al., 2007; Stroeymeyt et al., 2014)].

Nests, in particular, are likely to be extreme examples due to the elevated risks of disease transmission in densely populated, enclosed environments (Cremer et al., 2007; Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013). This may make selection to control disease transmission particularly strong on nest-building species. Similarly, the enclosed, controlled environment of a nest may offer more opportunities to construct it in ways that reduce the success of pathogen transmission (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Laland et al., 2017). This may include controlling air quality through fumigations or modifications to alter airflow, reducing energetic costs for those in the nest through protection from precipitation, wind, and temperature extremes (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Laland et al., 2017). For animals which live in cold environments, huddling behaviors can increase nest temperatures. Similarly, shaded nests may reduce energy costs in hot climates. These energy savings may enable individuals to invest more in immune defenses. At the same time, fumigations, building the nest with materials that have anti-parasitic properties, cleaning and anointing others, and removing waste and corpses likely reduce the quantity and diversity of pathogens (Octavio Lopez-Riquelme and Luisa Fanjul-Moles, 2013; Scott-Baumann and Morgan, 2015), effectively modifying the distributions of pathogens in the environment.

While nests are particularly visible examples, other species construct their environments as well. This includes changing the distributions of prey species through predation, distributing seeds and parasite larvae as they defecate, etc. (Laland et al., 2016, 2017). Animal behavior produces selection on their pathogens to adapt to environmental changes the animals bring about and this, in turn, generates selection on the host species, producing feedback loops (Laland et al., 2016, 2017). During human evolution, these feedback loops may have reduced selection pressure *against* social care, enabling increasing social care over time and greater pressure for pathogens to be controlled via community health behaviors (**Figure 1**).

Social Care in the Fossil Record

There are numerous fossil hominins which have been determined to have suffered from severe illnesses and disabilities, including Shanidar I with a severely damaged right arm and Aubesier 11 with severe tooth loss (Dettwyler, 1991; Lebel et al., 2001; DeGusta, 2003; Hublin, 2009; Spikins et al., 2019). This has led to vigorous debates about whether fossil evidence is sufficient to infer social care. When researchers have suggested that various conditions were so debilitating that it would have been impossible for the individual in question to survive without care, primatologists have frequently rebutted these arguments with evidence that wild primates survive similar afflictions without care. This has included primate populations where individuals recover from limbs being maimed or severed in snares (Byrne and Stokes, 2002; Munn, 2006; Stokes and Byrne, 2006; Beamish and O'Riain, 2014) and nearly complete tooth loss (Cuozzo and Sauther, 2004). However, while our understanding of wild primates' resilience makes it difficult to argue that these hominins definitely received care (Dettwyler, 1991; Byrne and Stokes, 2002; DeGusta, 2002, 2003; Cuozzo and Sauther, 2004; Munn, 2006; Stokes and Byrne, 2006; Beamish and O'Riain, 2014; Turner et al., 2014), our knowledge of the types of care-giving provided by primates (and indeed more distant taxa, citations above) make it equally difficult to argue that hominins definitely did not provide care (Lebel et al., 2001; Hublin, 2009; Spikins, 2015; Spikins et al., 2018, 2019). While we do know that sometime between diverging from our last common ancestor with chimpanzees and today, hominins scaled up the care we give to others, we still cannot say exactly when that occurred.

We also still do not know how and when hominins began exhibiting increasing community health behaviors; however, the Hominin Pathogen Control Hypothesis (**Figure 1**) predicts that after social care and community health behaviors appeared in the human lineage, they should have been interdependent and increased together.

Did Domestication Play a Role in the Evolution of Human Care?

Domestication itself does not appear to produce care-giving behaviors, in that when a species is domesticated, it does not appear to start providing care that the wild counterpart did not. However, the processes that humans underwent as we domesticated other species (Zeder, 2016, 2017), and possibly also ourselves (Hare, 2017), may have contributed to our cognitive predisposition to provide care and engage in extensive niche construction (Zeder, 2016, 2017).

Humans not only domesticated other species, but we have also been argued to have domesticated ourselves (Hare et al., 2012; Hare, 2017). We show some of the classic signs of domestication, including increased cooperation, communication, tolerance, prosociality, extended juvenile periods, and pedomorphic features (Hare et al., 2012; Hare, 2017; Benitez-Burraco and Kempe, 2018). Today 70–90% of care-giving is given within family networks (Kleinman, 1978). Since human social cognition is specialized for recognizing subtle changes in those we know well, we are particularly well positioned to notice when family members are ill (Kessler et al., 2017). We may hear respiratory infections in voice changes, see rashes or flushing from fever on faces, notice lethargy or signs of pain during movement, or blood shot eyes around in our white scleras (Provine et al., 2011; Fisher et al., 2014). Recent studies (Shakhar and Shakhar, 2015; Steinkopf, 2015; Tiokhin, 2016; Shakhar, 2019) have put forward provocative hypotheses suggesting that human symptoms are signals that evolved to influence care-giving and avoidance behaviors of others. This would be an exciting avenue for future research into if and how humans may be specialized for soliciting and providing social care. Thus, while human social cognition may have increased our ability to detect when those around us need care, the emotional and psychological changes associated with self-domestication (Hare et al., 2012; Hare, 2017) and cooperatively raising young (sensu Hawkes et al., 1998; Burkart et al., 2009; Hrdy, 2009; Tomasello, 2014) may have increased the likelihood that we would provide that care.

Domestication has been argued to be a type of niche construction (Zeder, 2016). While humans began domesticating plants and animals in the Neolithic, evidence suggests that we were dramatically altering the distribution of species on the landscapes on which we lived, going back to the disappearances of large megafauna in the Late Pleistocene (Boivin et al., 2016). In doing so, we likely altered the communities of pathogens that depended upon these species as well (Boivin et al., 2016). If so, it would suggest that human niche construction was extensive enough that it may have influenced pathogen communities long before agriculture and the breeding of domestic livestock in the Neolithic (Boivin et al., 2016).

Humans began domesticating other species in the Neolithic and since then, we have domesticated vast numbers of plants and animals (Boivin et al., 2016). We have dramatically altered and constructed our ecological niche, changing both the distributions of target species (prey species which became livestock, wild crops which became agriculture crops, and "pest" species) (Boivin et al., 2016). In doing so, we altered the biodiversity of pathogen communities that the domesticates evolved with, including diseases that can be zoonotic to humans, vector species attracted to livestock, commensal species like mice, etc. (Boivin et al., 2016). This meant that we likely re-engineered the distribution of pathogens in our environments, including creating high densities of our domesticated species and living at higher densities ourselves (Boivin et al., 2016). This probably created selection for controlling pathogens that spread through human populations or species on which we depended. In addition, humans also began constructing and living in shelters which likely created selection for disease control and "nest hygiene" in human communities, similarly to in birds and insects.

At this point, it is not possible to tease apart exactly what changes in human evolution produced the healthcare behaviors we see in humans today. Instead of being one causal factor, it seems more plausible that when we look across animals there are a number of things that increase the likelihood of healthcare behaviors evolving: extensive niche construction (Boivin et al., 2016), expanded kin networks and extended juvenile period (Hawkes et al., 1998; Burkart et al., 2009; Hill et al., 2009; Hrdy, 2009), cooperative behaviors (Tomasello, 2014), and increased cognition and communication (Benitez-Burraco and Kempe, 2018; Benitez-Burraco et al., 2018). Thus, human care-giving may reflect the integration of two distinct types of healthcare behaviors each with its own evolutionary history (1) selection to provide social care to those in our social networks and (2) selection to construct our niches in ways that facilitate the control of pathogens.

Interestingly, work on the evolution of eusociality in insects suggests that the evolution of social immunity behaviors may have been a prerequisite to the evolution of the high density eusociality seen today (Meunier, 2015). This raises the possibility that the same may have been true in humans – that social care and community health behaviors may have enabled later increases in human density and social complexity (Kessler et al., 2018).

Summary and Future Directions

This paper provided a novel synthesis of animal care-giving in sickness contexts. I reviewed both social care behaviors which are directed at the sick individual and community health behaviors which benefit the community by controlling pathogens in the environment. In examining the mosaic of behaviors present across species, it appears that social care may have evolved in association with offspring care systems while community health behaviors may have evolved convergently in several taxa that engage in striking niche construction behaviors, like nest building. Finally, I introduced a novel hypothesis, the Hominin Pathogen Control Hypothesis, which predicts that human healthcare evolved through the integration of social care and community health behaviors. Aspects of this hypothesis could be tested in several ways:

(i) Test whether levels of social care and levels of community health behaviors covary, such that higher levels of one type of healthcare behavior should be associated with higher levels of the other. This could be tested across populations, i.e., nests within a species, or across species. Note that it would not be necessary for the same individuals who engage in social care to also engage in community health behaviors. The two types of healthcare behaviors could be carried out by different individuals. However, if the two types of healthcare behaviors do covary across populations or species, it would support the idea that they are linked.

(ii) Examine whether other taxa known for elaborate niche construction, also engage in community health behaviors.

This would support the idea that community health behaviors are a form of niche construction.

(iii) Conduct a comparative study using researcher surveys of when opportunities for social care were present and no care was given. A more systematic understanding of which species provide social care and how often would enable a quantitative analysis of how social care may overlap with different infant rearing systems. These results could support the idea that social care is rooted in offspring care systems.

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SK wrote the manuscript and agreed to be accountable for the content of the work.

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Human Social Evolution: Self-Domestication or Self-Control?

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The self-domestication hypothesis suggests that, like mammalian domesticates, humans have gone through a process of selection against aggression – a process that in the case of humans was self-induced. Here, we extend previous proposals and suggest that what underlies human social evolution is selection for socially mediated emotional control and plasticity. In the first part of the paper we highlight general features of human social evolution, which, we argue, is more similar to that of other social mammals than to that of mammalian domesticates and is therefore incompatible with the notion of human self-domestication. In the second part, we discuss the unique aspects of human evolution and propose that emotional control and social motivation in humans evolved during two major, partially overlapping stages. The first stage, which followed the emergence of mimetic communication, the beginnings of musical engagement, and mimesis-related cognition, required socially mediated emotional plasticity and was accompanied by new social emotions. The second stage followed the emergence of language, when individuals began to instruct the imagination of their interlocutors, and to rely even more extensively on emotional plasticity and culturally learned emotional control. This account further illustrates the significant differences between humans and domesticates, thus challenging the notion of human self-domestication.

Keywords: self-domestication hypothesis, human social evolution, language evolution, music evolution, emotional control

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INTRODUCTION

The notion that humans are "domesticated" far precedes the notion that humans have evolved. Since antiquity, scholars have described humans (in general or in reference to their own particular culture) as domesticated, which generally referred to their "civility": their distance from a wild or savage state of being. It was common for writings on the subject to be entangled with various value judgments, with some considering the superiority of a domesticated state, while others described it as a kind of physical and mental degeneration. Coupled with the tradition of differentiating human cultures on the basis of the extent to which they were "domesticated," much literature on the subject promoted views of social hierarchies in civility, which were later used as a pseudo-scientific rationale for racist and eugenic political movements (reviewed in Brüne, 2007). This stain on the intellectual history of human domestication theories illustrates the complex social meanings of the concept, and its consequent ambiguity when used in explaining human evolutionary processes.

It was Darwin who first critically discussed self-domestication from an evolutionary perspective. While he conceded that humans are similar to domesticates in exhibiting extreme phenotypic variability, he nonetheless argued that the term domestication would be misapplied in the case of human evolution:

> "It is, nevertheless, an error to speak of man, even if we look only to the conditions to which he has been exposed, as 'far more domesticated' [. . .] man differs widely from any strictly domesticated animal; for his breeding has never long been controlled, either by methodical or unconscious selection. No race or body of men has been so completely subjugated by other men, as that certain individuals should be preserved, and thus unconsciously selected, from somehow excelling in utility to their masters." (Darwin, 1871, pp. 28–29)

That said, Darwin's study of domesticated species recognized the package of traits that many mammalian domesticated species share, which includes morphological traits such as skeletal changes (shorter muzzle, decreased heart size, reduced teeth size, short and curly tail, floppy ears), physiological traits such as altered and usually more numerous reproductive cycles, and the retention of many juvenile behavioral features. Decades later, Boas (1938) observed that many of these traits were also shared by humans, and suggested that this was due to similar selective pressures. Specifically, Boas suggested that in both cases, traits like de-pigmentation, shortening of the face, and the loss of reproductive periodicity were partially the result of a more protective environment and a diet of softened, processed food. Notably, Boas argued that various social laws and prohibitions (e.g., marriage regulation, prohibition of infanticide) could also have had selective effects, and was thus anticipating concepts like cultural niche construction, which would later prove crucial for understanding human evolution.

In 1959, a still-ongoing experiment on the domestication of silver foxes was initiated by Dmitri Belyaev, Lyudmila Trut and their colleagues in Novosibirsk (Belyaev, 1979; Trut, 1999; Trut et al., 2006; Dugatkin and Trut, 2017). Belyaev's experimental design has become central to the current formulation of the self-domestication hypothesis. Belyaev defined domesticated behavior as "the ability of animals to have direct contact with man, not to be afraid of man, to obey him, and to reproduce under the conditions created by him" (Belyaev, 1979). The experimenters consequently selected for tameness – the degree to which human contact resulted in docile, rather than aggressive, behavior. Tameness was estimated through limited human contact: a gloved hand was introduced into a cage with a young fox cub, and its reaction was monitored (Trut et al., 2009). Importantly, the procedure did not involve any prolonged contact or training, and selection was based purely on the perceived propensity toward tame behavior. Belyaev thus separated as best he could the genetic component, and created a speeded up evolutionary process. It should be stressed, however, that during typical processes of social evolution, including domestication, selection is much more complex and taming includes many additional factors, including priming and learning processes. In the case of human social evolution, these involve social and cultural interactions within and between groups.

It is also important to note that the original fox population used in Belyaev's experiments had been bred in captivity for about 50 years before the domestication experiment was initiated, so the farm foxes do not represent a completely wild population (Lord et al., 2019). Most of the foxes were either aggressive, fearful, or aggressively fearful in response to human contact, but a few displayed less aggressive and more exploratory reactions toward the gloved hand (Belyaev, 1979). About 10% of the most tame in each generation were selected (Trut et al., 2009). Several generations later, the experiment had produced a population of foxes whose reaction to human contact was the opposite of that exhibited by most of the original population, with fear and aggression superseded by willful and positive engagement. As predicted by Belyaev, the behavioral changes were accompanied by physiological and morphological changes, as well as by changes in mating habits. The foxes had shortened legs, tails, snouts and upper jaws; floppy ears, curly tails, and altered coat color patterns; mating became more frequent and no longer strictly seasonal; supernumerary and non-essential B chromosomes became more frequent; the pattern of inheritance of a pigmentation pattern (a white star on the forehead) was found to be non-Mendelian. At the hormonal level, which is involved in many behavioral changes, the domesticated population exhibited reduced activity of the Hypothalamus Adrenal Axis (HPA axis), as well as higher levels of serotonin and higher activity of key enzymes related to serotonin synthesis and degradation, both of which appear to be critical for the facilitation of tame behavior. Interestingly, a line of foxes selected for increased emotional reactivity (enhanced fearful-aggressive behavior) also showed some characteristics of the domestication syndrome (white spotting and changes in stress hormones), suggesting that different variations in the regulation of the same developmental pathway may have been under selection in both the tame and the aggressive lines. The fox selection experiments are reviewed in Jablonka and Lamb (1995); Markel and Trut (2011), Dugatkin and Trut (2017), Wilkins (2017, 2019), and Lord et al. (2019).

Discussions of self-domestication since the late-20th century have centered around Belyaev's definition of domestication – in particular, his emphasis on tameness and reduced aggression rather than adaptation to human-made environments. Later research has put into question the robustness of his definition. Lord et al. (2019) argued that the evidence for a widely shared suite of traits among animal domesticates, a "domestication syndrome" (DS)[1], is inconclusive: none of the DS traits are shared by all domesticates, although a reduction in brain size, changes in craniofacial characteristics and increased variation in coat color are observed in most. Nevertheless, in general there is a "family resemblance" among domesticated species, which, we believe, renders the notion of DS useful (but see Lord et al., 2019 for a dissenting view).

Coppinger and Coppinger (2001) proposed a different route to domestication from that of Belyaev. They suggested that the domestication of wolves (*Canis lupus*) into dogs involved an initial phase in which less nervous members of the group

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[1] The term "domestication syndrome" (DS) was first used to describe the suite of characters shared by animal domesticates by Wilkins et al. (2014).

became better dump-feeders in human habitats, and eventually formed a separate population. During this stage there was "self-domestication," which involved adapting to feeding opportunities in and near human habitats (becoming a synanthropic species), initially without intentional human intervention.

Hare and colleagues have suggested that bonobos (*Pan paniscus*) have also undergone self-domestication, meaning, more generally, that they went through a process in which selection for reduced aggression led to DS traits (Hare et al., 2012; Hare, 2017). Citing evidence for reduced aggression and physiological and morphological differences between bonobos and chimpanzees (e.g., Rilling et al., 2012), Hare and colleagues proposed a model of bonobo evolution involving the formation of female coalitions, which thwarted male aggression and male alliances. They called the outcome of this process of selection against aggression "self-domestication." While reduced aggression (seen in less competitive feeding habits and increased social tolerance) is emphasized, other critical behavioral factors are also mentioned. These include more stable parties, extended female sexual receptivity and a much less significant reduction in relative brain size (when compared to species domesticated by humans). This raises the question of whether this complex suite of physiological traits and social behaviors is indeed best described as an outcome of a "self-domestication" process, rather than as the outcome of selection for cooperation and emotional control that is observed in many other highly social mammals. In the case of humans, these questions are particularly pertinent.

Human self-domestication is usually characterized as a process of selection against aggression, and more recently as selection for pro-sociality. For example, Sánchez-Villagra and van Schaik (2019) characterize the human self-domestication hypothesis (HSD) thus: "The current version of the HSD hypothesis postulates that selection for reduced aggressiveness in human evolution led to physiological, psychological, and behavioral changes, specifically to social tolerance (p. 136)." Hare (2017), who recognizes the importance of selection for self-control in human evolution, also emphasizes the similarities of human social evolution to that of domesticates and stresses selection for pro-sociality and against aggression: "The human self-domestication hypothesis (HSD) draws on comparative, developmental, fossil, and neurobiological evidence to show that late human evolution was dominated by selection for intragroup pro-sociality over aggression (p. 157)." The stress on selection against aggression and for docility is also highlighted by Francis (2015), and with qualifications, by Wrangham (2018), who focuses on a reduction in reactive, high arousal, non-calculated aggression.

Hare (2017) underscored the complexity of the changes undergone by humans and suggested that increased self-control is the hallmark of human social and cognitive-affective evolution. We agree with this suggestion, which was based on Hare and Tomasello's earlier proposal that a reduction in emotional reactivity was the pre-condition for human cognitive evolution (Hare and Tomasello, 2005). In the second part of this paper we extend these suggestions and propose that engagement in music and in linguistic communication contributed significantly to the evolution of cognitive and emotional plasticity in the genus *Homo*. However, because of the differences between humans and domesticates, we take issue with suggestions that human social evolution, especially early evolution, is best described in terms of self-domestication. We suggest that the evolution of unique human characteristics requires an explanatory framework based on emotional and cognitive plasticity, a framework that goes beyond the selection against aggression and for pro-sociality that is described in most characterizations of self-domestication.

Other accounts of HSD stress the similarities in the protective environments of humans and their domesticated species (Thomas, 2013), emphasizing the effects of relaxed selection pressures on both human and domesticate evolution (Brüne, 2007). Our approach differs from these accounts by (1) focusing on earlier hominin evolution, beginning with *Homo erectus*, when most human-specific cooperative and morphological traits seem to have already evolved; (2) suggesting that human social evolution is more similar to the evolution of pro-social behavior in other highly social mammals, which is associated with increased sophistication of social structures and increased cognitive and emotional plasticity; and (3) emphasizing the unique social-cultural selective environment of humans, which, we argue, shaped and amplified our species' cognitive and affective plasticity. The recent evolution of humans, especially after the split with Neanderthals, is interpreted as the outcome of intense cultural evolution driven by language, musicking and other cultural strategies (Heyes, 2018), rather than by selection against aggression.

SIMILARITIES AND DIFFERENCES BETWEEN HUMANS AND DOMESTICATES

The HSD hypothesis is based on the assumption that since humans share several (though not all) traits common to many animal domesticates, they have undergone a similar selection process (Thomas and Kirby, 2018). In addition to morphological and behavioral similarities, there is also some evidence that selection targeted genes in the same developmental pathways, including genes expressed in neural crest cells. Wilkins et al. (2014) suggested that gene mutations leading to slightly reduced expression of genes in the neural crest underlie the DS and can explain why so many traits are shared among domesticates. Neural crest cells are pluripotent embryonic cells, derived from the neural tube in early embryogenesis. The cells migrate and give rise to neuroendocrine cells, pigment cells, neurons and glial cells of the sensory, sympathetic, and parasympathetic nervous systems and many of the skeletal and connective tissue components of the head. Since the structures and processes associated with the neural crest are also related to the DS traits, the hypothesis offers a unifying explanation. Genetic variation in the regulatory genetic networks (GRNs) of these pathways have indeed been shown to characterize several domesticates (Simões-Costa and Bronner, 2015; Theofanopoulou et al., 2017; Wilkins, 2019). Moreover, variation in neural crest genes, as well as variations in genes expressed in cortical regions of the brain (including the neo-cortex) have been observed in neurodevelopmental pathways that affect neural plasticity and learning (see Theofanopoulou et al., 2017 for a comparison focusing on humans, and Wang et al., 2018 for gene expression in silver foxes).

In addition to variations in DNA base sequences, epigenetic variations may also be involved in the DS, since it was shown that the expression of the DNA methyltransferase genes differs between domesticated and control foxes (Herbeck et al., 2017). There is also evidence of significant and multiple epigenetic differences between jungle fowl and domesticated chickens: selection for fearful and non-fearful behavior in the jungle fowl for only five generations led to divergent DNA methylation in 22 genomic regions in hypothalamus cells, some of which were associated with neural functions and cellular metabolic pathways relevant to the stress response (Bélteky et al., 2018). A study of very recent domesticates of sea bass, which show no genetic differences from wild fish, found that these recent domesticates have epimutations (differences in patterns of DNA methylation) in various tissues, with about one fifth of the persistent epimutations being in genes that are expressed in embryonic structures, including the neural crest. Furthermore, the epimutated genes coincide with mutated genes in established domesticates (Anastasiadi and Piferrer, 2019). It is therefore plausible that a comparative study of epigenetic (e.g., methylation) differences among domesticates and humans will reveal many more substantial similarities and differences than gene-sequence differences, but at present there are only a few comparative studies that address this question.

Table 1 presents a comparison between human traits that correspond to traits that are said to characterize the DS in (i) apes (bonobo compared to chimpanzee), (ii) dogs/wolves (feral and domestic dogs compared to the gray wolf), and (iii) foxes selected for tame behavior and wild, unselected ones. A detailed comparison of the traits associated with DS that includes many other species of domesticates is presented and discussed in Sánchez-Villagra et al. (2016).

The table shows some similarities between humans, bonobos, dogs and tame silver foxes that conform to the characteristics of the DS. The levels of behavior-affecting hormones, most notably elevated levels of serotonin and oxytocin, which are correlated with reduced emotional reactivity, are increased in humans, dogs and tame foxes, with tame and wild foxes showing clear differences with regard to the genes involved in these pathways (Wang et al., 2018). Another similarity is the juvenilization of morphology, the increase in morphological variation, and the prolonged play period in humans and domesticates. These similarities are thought to reflect parallel evolution affecting the same set of genetic regulatory networks in humans and domesticates, in particular, though not exclusively, in genes controlling developmental networks in which neural crest cells are involved. The data, however, are far from conclusive. When genes showing adaptive sweeps in modern humans (742 human genes) and domesticates (dog, cat, horse, taurine cattle; 691 genes in total) were compared, 41 were shown to be shared by both humans and one or more domesticated species (15 of the 41 were shared with the dog), and only 5 of the 41 were shared between humans and several domesticates. Of these 5 genes, 4 showed variations related to neural, behavioral and morphological characteristics related to the DS and to neural crest pathways. Two genes seem particularly important: BRAF, which affects learning and neural plasticity, and GRIK3, which affects both learning and cranial characteristics (Theofanopoulou et al., 2017). However, as Theofanopoulou et al. (2017) point out, the human data are based on somewhat contested compilations of human genes showing adaptive sweeps. There are also important data limitations that complicate interpretation: identification of adaptive sweeps uncovers selective changes only in protein coding genes, so the regulatory non-coding sequences, which are probably of the greatest significance in the evolution of the relevant regulatory networks, cannot be detected. This means both that the number of overlaps is likely to be underestimated, and that the overlaps identified may not be specific to the DS.

We do not want to downplay the similarities between humans and domesticated foxes and dogs, nor do we question the involvement of neural crest mutations in the DS. We believe, however, that these commonalities can be explained in a way that is not committed to the HSD hypothesis. The neural crest pathways affect such a large suite of morphological, physiological and neural phenotypes that we expect that variations in them will be targeted by social selection whenever there is strong selection for altered emotional reactivity, mate selection, and social cognition – that is in *several* social selective contexts. These include selection for domestic, tame characteristics; selection reducing stress-related behaviors involving the flight (fear) and fight (aggression) responses seen in small island populations of newly introduced animals; sexual selection and social selection for pro-sociality in social mammal and bird groups; and social-cultural selection for human cognition and affect. Sexual selection and changes in diet and climate can also be underlain by variations in developmental processes that involve the neural crest, which lead to cranial modifications such as those seen in Neanderthals and Denisovans.

The table clearly shows that as well as similarities there are also striking differences between humans and domesticates. One important trait that humans do not share with most (80%) domesticates is reduced brain size – in fact, the opposite evolutionary trend is often considered as a hallmark of human evolution. While reduced cranial capacity is in line with other pedomorphic traits of domesticates, an increase in hominin brain size relative to body size has been correlated with changes in diet resulting in higher energy intake, increased technical intelligence, and greater social complexity (Dunbar, 1998; Barton, 2012; DeCasien et al., 2017). The retention of juvenile traits in humans is associated with increased, rather than decreased, brain size because the extended human juvenile period involves a prolongation of neural growth and development (Gould, 1996). As noted by Spurway (1955) in her seminal paper on domestication, the reduced brain size of domesticates can be explained as the result of selection for the breakdown of social structures. To encourage increased growth and reproduction in domesticates, humans selected for the slackening of mating criteria, a shorter period of parental care, reproduction at earlier ages, unresponsiveness to group hierarchy, less discrimination in the choice of food, less territorial defense, and so on. These traits

TABLE 1 | Comparison between modern humans, apes, and domesticated and non-domesticated canids (dogs/wolves and tame/wild foxes).

Species evolved factors	Modern humans	Bonobo/chimpanzee	Dog/wolf	Domesticated silver foxes/unselected foxes
Morphology				
Morphological variability	Highly variable	Both species less variable than humans	Dog breeds highly variable	Tame foxes highly variable
Mean brain volume (cm^3)	1239.8; increase in human brain size throughout most *Homo* evolution; 10% reduction during the last 10,000 years[1]	345.6/375.1[1]	100.4/139.8[2]	Negligible differences[3]
Cranium	Evolved globularity emerged in *H. sapiens* lineage[4]	Average bonobo endocranium is more rounded and less elongated than that of the chimpanzee[5]	Reduced facial length in dogs compared to wolves[6]	Changes in the tame strain are similar to changes during dog's early domestication[7]
Sexual dimorphism in body mass (male/female ratio)	1.16[1]	1.35/1.31[1]	Varies with size of dog breed; 1.27 in wolves[8]	1.2 in wild red fox[9]; no available data on experimental groups
Pigmentation	Depigmentation of the sclera is unique to humans[10]	Depigmentation of lips and tail tuffs in bonobos[11]	Depigmentation of coat in dogs[12]	Depigmentation of coat in tame foxes[7]
Endocrinology				
Serotonin receptor	Receptor expression in the amygdala's central and accessory basal nuclei is significantly higher compared than in the chimpanzee and bonobo (*Pan*) genus[13]	Receptor expression in amygdala's basal nuclei is significantly higher in bonobos[14]	High levels of variation in serotonin receptor and transporter genes of the dog[15]	Higher levels of serotonin and serotonin receptors in the brain of tame foxes[16]
Oxytocin receptor	Genetic variation linked with social behavior, empathy and autism[17]; epigenetic changes in oxytocin receptor gene associated with autism and unemotional traits[18]	Fixed genetic variation in both species compared with the polymorphisms found in humans; five additional genetic polymorphisms found in chimpanzees but not in bonobos or humans; their functional importance has not been determined[19]	Genetic variation in dogs related to differences in social behavior[20], was not identified in wolves[21]; epigenetic differences among dogs associated with differences in appeasing behavior[22]	No available data
Prolactin	Adult male prolactin levels rise in response to infant cries during fatherhood and during participation in sexual acts[23]	Prolactin levels in male chimpanzees spike throughout sexual development[24]; no available data on bonobos	Prolactin levels rise in all wolf pack members during pup-rearing period[25], but are not correlated with paternal behavior in male dogs[26]	No available data
Cortisol	Cortisol levels are sensitive to environmental conditions and are socially regulated during postnatal development[27]	Cortisol levels in bonobos, but not in chimpanzees, change during competition over food and show a greater increase in response to social stressors[28]	Baseline cortisol levels in wolves depend on dominance hierarchies[29], whereas in dogs they are sensitive to human caregivers' personality and lifestyle[30]	Reduced cortisol levels in all tame strains; highly reduced in pregnancy and lactation[31]

(Continued)

TABLE 1 | Continued

Species evolved factors	**Modern humans**	**Bonobo/chimpanzee**	**Dog/wolf**	**Domesticated silver foxes/unselected foxes**
Testosterone levels in males	Increase during out-group competition; decrease during in-group competition, pair-bonding and co-sleeping with child[23]	In male chimpanzees but not bonobos, there is pubertal and adulthood increases and level-changes during competition over food[32]	Increased testosterone in wolves is seasonal and tied to reproduction, whereas most dog breeds continuously maintain elevated levels [33]	Lower levels of plasma testosterone in tame foxes[34]
Variation in DNA and in gene expression	Humans show many differences when compared to apes; there are also differences between anatomically modern humans and archaic humans; archaic humans do not show adaptive sweeps in genes related to DS characteristics[35]	The observed divergence of neural and social traits in chimpanzees and bonobos has not been associated with differences in protein patterns[36]	Overlap among 15 genes that show adaptive sweeps in both modern humans and dogs (but not in wolves). Of these 4 genes show characteristics associated with the DS[35]	150 genes show different patterns of expression in lines of foxes selected for aggression and tameness; allele frequencies at 176 gene loci, including genes associated with neural crest functioning, are different between the aggressive and tame lines[37]
Emotional reactivity				
Aggression	Compared to other primates, humans show high propensity for proactive aggression and low propensity for reactive aggression[38]	Both proactive and reactive aggression in chimpanzees; reduced proactive aggression and reduced severity of reactive aggression in bonobos[39]	Both species show only rare and weak aggression among conspecifics[40]	Tame foxes are very docile and non-aggressive compared to control group[41]
Cooperativeness (pro-sociality)	Early onset of cooperative and pro-social behavior[42]	Cooperation in chimpanzees is limited, and restricted to same-sex pairings whereas bonobos show broader cooperation[43]	Compared to wolves, dogs find it difficult to cooperate with conspecifics [44]	Tame foxes are more interested in interacting with humans than are wild foxes[41]
Emotional control	Humans can either inhibit, modulate or mobilize aggressive and other emotional responses, depending on ecological conditions, norms etc. [45]	Bonobos are more socially tolerant than chimpanzees[46]	Dogs show a higher level of inhibitory control than wolves with regard to humans, and can better suppress their immediate drives in favor of delayed rewards[47]	Compared to wild foxes, tame foxes show an increase in exploratory behavior with age, coupled with a substantial decrease in cortisol levels[48]
Life History				
Neotenous features	Observed across various anatomical traits of adult humans[49]; gene expression indicates neural neoteny in brain areas involved with social and cognitive skills[50]	Bonobos have pedomorphic cranium, white tail-tufts that characterize juvenile chimpanzees, and play between adults is similar to adult-juvenile chimpanzee play[51]	Dog breeds are underdeveloped to varying degrees with regard to physical and behavioral traits compared to wolves[52]	Tame foxes show a trend for faster sexual maturation accompanied by retarded development of some somatic traits[7]
Length of female reproductive cycle (years)	3.05[53]	4.8/5.2–6.6[54]	0.45/0.7[55]	0.5–1/1[7]
Length of juvenile period (years)	13.3[56]	12/7.2[56]	Juvenile period is similar in both species, but wolves' sexual maturity may depend on growth in size and on territoriality[57]	Sexual maturation in tame foxes occurs a month earlier on average[7]

(Continued)

TABLE 1 | Continued

Species evolved factors	**Modern humans**	**Bonobo/chimpanzee**	**Dog/wolf**	**Domesticated silver foxes/unselected foxes**
Social behavior and cognition				
Developmental timing	Long childhood; human brains show an extreme level of postpartum development, followed by an extended period for synaptic pruning that lasts until the mid-20's[58]	Extended development and maternal-attachment in bonobo infants, with delayed development of social behavior and cognition relative to chimpanzees[59]	The period of socialization in domestic dogs is longer than that observed in wild or socialized wolves[60]	Sensitive period for social development in tame foxes is extended from 45 days to 12 weeks or longer[41]
Reproductive regulation	Mating and child rearing are regulated by cultural group norms[61]; concealed copulations occur regardless of male dominance and status[62]	Reproduction is determined by dominance hierarchies in chimpanzees[54], whereas in bonobos male reproductive success is influenced by mother's social status[63]	Reproduction in dogs is controlled by humans; in wolves, the dominant pair breeds while other females are reproductively suppressed, unless food is abundant[64]	Reproduction of tame foxes controlled by humans; in ancestral wild species, female reproduction depends on population density, food supply, and social status[65]
Paternal care	Variable across-cultures and associated with local ecologies and social environments[66]	Similar patterns in both *Pan* species, but bonobo males engage in more playful activity with infants, including sociosexual play[67]	Male wolves provide babysitting and play with infants, whereas provisioning by male dogs is rare and limited[68]	Males in wild populations defend and provision pups[69]; no available data on experimental groups
Alloparenting	Modern humans in hunter-gatherer groups and other social organizations practice alloparenting[61]	Bonobos show more allomaternal care than chimpanzees[70]	Helpers in wolf packs attend to, and provide for pups[64]; provisioning by non-maternal female dogs is rare[57]	Females act as helpers in wild populations[71]; no available data on experimental groups
Infanticide	Relatively rare in hunter-gatherer groups and usually initiated by the mother, when resources are limited or the infant is deformed[61]	Male bonobos assault, but do not attempt to kill, weaned offspring; male chimpanzees commit infanticide[72]	Major mechanism used by dominant feral dog females to suppress reproduction of subordinates; dominant female wolves aggressively prevent copulation by subordinates[73]	Not reported for experimental groups; in farm conditions, infanticide by vixens is correlated with more tense and insecure behavior[74]
Communication and information sharing	Polymodal and variable communication; extensive information sharing and early manifestation of communicative intents and skills[75]	Compared to chimpanzees, bonobos are more sensitive to human gaze direction, use indexical cues in the vegetation when foraging in small groups, and acquire better linguistic skills in experimental settings[76]	Wolves have better skills with regard to gaze following and imitation vis á vis conspecifics, but only dogs gaze at human faces for assistance[77]; both follow human pointing but it appears earlier in dogs than in wolves[78]	Tame pups more skilled in responding to human communicative gestures; novel displays of tail wagging, submissive posturing and barking in adult tame foxes[79]
Play	Advanced pretend play parallels language development[80]; social and pretend play in hunter-gatherers are used to counteract tendencies toward dominance[81]	During juvenile period play-fighting becomes longer and more cooperative in bonobos, whereas in chimpanzees it is more competitive[82]	Juvenile play behavior is maintained in adult dogs[83]	Play during adulthood is more common in tame foxes[84]

[1] MacLeod et al., 2003; Robson and Wood, 2008; Bednarik, 2014; [2] Comparison taken from dog breed and wolf with similar body masses; see Smith et al., 2018; the variability between different strains should, however, be noted; Lord et al., 2019; [3] Trut et al., 1991 (quoted in Wilkins et al., 2014); [4] Neubauer et al., 2018; [5] Durrleman et al., 2012; [6] Franciscus et al., 2013 (quoted in Cieri et al., 2014); [7] Trut et al., 2004; [8] According to Frynta et al., 2012, Sexual size dimorphism in large breeds is comparable to SSD of wolf; becomes smaller with decreasing body size (see also Moehlman and Hofer, 1997); [9] Voigt, 1987; [10] Tomasello et al., 2007; [11] Kano, 1992; [12] Coppinger and Coppinger, 2001; [13] Lew et al., 2019; [14] Stimpson et al., 2016; [15] van den Berg et al., 2005; [16] Popova et al., 1991; [17] Wu et al., 2005, 2012; Tost et al., 2010; [18] Kumsta et al., 2013; [19] Staes et al., 2014; [20] Kis et al., 2014; [21] Oliva et al., 2016; Bence et al., 2017; [22] Cimarelli et al., 2017; [23] Gray et al., 2017; [24] Kondo et al., 2000; [25] Kreeger et al., 1991; Asa, 1997; [26] Corrada et al., 2003; [27] Gunnar and Donzella, 2002; Flinn et al., 2011; [28] Wobber et al., 2010a; [29] Sands and Creel, 2004; [30] Schöberl et al., 2017; [31] Trut et al., 2009; [32] Wobber et al., 2010a, 2013; [33] Asa, 1997; [34] Osadchuk and Shurkalova, 1992; [35] Theofanopoulou et al., 2017; [36] Staes et al., 2019; [37] Wang et al., 2018; [38] Wrangham, 2018; [39] Surbeck et al., 2011; Furuichi, 2011; [40] Range et al., 2015; [41] Trut, 1999; [42] Tomasello, 2009; [43] Surbeck et al., 2017; [44] Feddersen-Petersen, 2007; [45] Hare, 2007; Jablonka et al., 2012; [46] Tan and Hare, 2017; Hare et al., 2007; [47] Gácsi et al., 2009; Marshall-Pescini et al., 2015; [48] Trut, 2001; [49] Skulachev et al., 2017; [50] Bufill et al., 2011; [51] Wrangham, 2002; Palagi, 2006; Lieberman et al., 2007; [52] Udell et al., 2010; [53] Key, 2000; [54] Gruber and Clay, 2016; [55] Jöchle, 1997; [56] Jones et al., 2009; [57] Lord et al., 2013; [58] Zollikofer and Ponce de León, 2010; Casey, 2015; [59] de Lathouwers and Van Elsacker, 2006; Wobber et al., 2010b; [60] Coppinger and Coppinger, 2001; Gácsi et al., 2009; [61] Hrdy, 2009; [62] Ben-Mocha et al., 2018; [63] Surbeck et al., 2019; [64] Montgomery et al., 2018; [65] Macdonald, 1980; [66] Fernandez-Duque et al., 2009; [67] Enomoto, 1990; [68] Kleiman and Malcolm, 1981; Pal, 2005; [69] Macdonald, 1979; [70] Kano, 1992; Furuichi, 2011; [71] Moehlman and Hofer, 1997; [72] Gottfried et al., 2019; [73] Corbett, 1988; [74] Braastad, 1987; Braastad and Bakken, 1993; [75] Tomasello, 2008; [76] Savage-Rumbaugh et al., 1996; Gillespie-Lynch et al., 2014; MacLean and Hare, 2015; [77] Range and Virányi, 2013, 2014; [78] Gácsi et al., 2009; [79] Trut, 1999; Hare et al., 2005; [80] Lewis et al., 2000; Hughes, 2010; [81] Gray, 2009; [82] Palagi, 2006; [83] Goodwin et al., 1997; [84] Trut, 2001; Trut et al., 2004, 2009.

are often associated with diminished perceptual acuity and lead to a social structure that is impoverished relative to that of their wild ancestors, and that is not self-sustaining in the absence of human provisioning (Avital and Jablonka, 2000).

There is evidence for a reduction in endocranial volume in humans in the past 40,000 years and especially the last 10,000 years (Bednarik, 2014), and it has been suggested that this points to selection for pro-sociality. Alternatively, the reduction may be related to the decrease in overall size, to increased sedentism, more reliable food availability and greater safety (Hare, 2017; Thomas and Kirby, 2018). It is, however, important to note that most morphological and behavioral traits that are associated with the DS in anatomically modern humans (e.g., increased social cooperation, neoteny, changes in cranial morphology, reduced sexual dimorphism) are shared by archaic humans, and so preceded the period in which HSD is supposed to have occurred.

There are certainly differences in human morphology as well as in genes when Neanderthals, Denisovans and anatomically modern humans are compared (Hare, 2017), and some changes are in genes affecting pathways in which neural crest cells are involved and that lead to changes in the cranium. In a recent study, Zanlella et al. (2019) showed that there were changes in the chromatin remodeler BAZ1B in neural crest stem cells during the evolution of anatomically modern humans. They found that large-effect mutations in the regulatory region of this gene lead to DS-like cranial and neural disease-related variation in modern humans. More subtle genetic variations in the regulatory regions in this gene differ between modern humans, Neanderthals and Denisovans and may be related to the cranial differences among them. The reduction in average brow ridge projection and shortening of the upper facial skeleton from the Middle Pleistocene to recent times has been linked by Cieri et al. (2014) to a reduction in aggression and increased social tolerance. However, the context in which these cranial and behavioral changes were selected is not clear, and it has not been established that they are the result of selection against aggression rather than, for example, the result of sexual selection, or changes in diet or climate. Finally, the data showing adaptive sweeps in modern humans but not in Neanderthals are very limited (Theofanopoulou et al., 2017). Nevertheless, it is possible that, as Sánchez-Villagra et al. (2016) have suggested, once humans had adopted a more sedentary life style, about 15,000 years ago, there was selection for decreased vigilance similar to that observed in animals that migrate to small islands devoid of predators, which often leads to reduced brain size. This may partially account for the recent reduction in human brain size.

A second important difference between humans and most other domesticates is the types of aggression they display. While humans can be docile and patient with one another in some situations, they can also be extraordinarily violent at others. Wrangham (2018) distinguished between reactive and proactive aggression in order to clarify this apparent oddity. Humans, he suggests, share with chimpanzees a high propensity for proactive aggression (purposeful, target-consistent, low arousal), and share with bonobos a low propensity for reactive aggression (responsive, target-inconsistent, high arousal). However, if self-domestication is defined as selection against reactive aggression, many social mammals, including meerkats and mole rats, should be included in the self-domestication category. Furthermore, when violence occurs, reactive and proactive aggression are often mixed (Allen and Anderson, 2017). Although the decision-mechanisms initiating proactive violence are claimed to be neurally distinct (Blair, 2016), levels of arousal may change during the act itself – a "coldly" premeditated act of violence can be carried out in a state of high arousal. The lower rates of within-group violence among humans compared to other great apes (Wrangham, 2018) may in part be a result of violence being better controlled, both emotionally and socially, rather than the propensity for reactive aggression being simply reduced.

A third crucial difference between humans and domesticates relates to the absence, in the case of humans, of subordination to another species, and an increased dependence on other group members with regards to foraging, hunting and alloparenting. Consider the differences in social ecology between wolves and dogs: dogs feed primarily on human waste, whereas wolves rely mostly on group hunting; dog pups are raised mostly by their mothers (and, in the case of pet dogs, by humans as well), while wolf pups are raised by the entire pack (Marshall-Pescini et al., 2017a). Recent experiments have clarified the impact of the different social ecologies on behavior, showing, for example, that wolves have greater pro-social tendencies toward pack members than do dogs (Dale et al., 2019), that they cooperate better with conspecifics than dogs (Marshall-Pescini et al., 2017b), and that although wolves and dogs are both capable of cooperating with familiar humans, dogs tend to take on more submissive roles (Range et al., 2019). Like wolves, throughout much of their evolutionary history humans relied on group-coordinated hunting and participated in alloparenting. Until the onset of agriculture, they did not rely on living alongside and being provisioned by another species, but rather on their intra-group pro-social tendencies, which allowed them to cooperate with one another. In other words, humans' social ecology did not require docility toward a domesticator, but rather emotional plasticity that can lead to condition-dependent pro-social behavior among group members, as well as highly aggressive behavior, mainly toward individuals belonging to other social groups. In many ways, human social evolution is more similar to that of wolves than to that of dogs.[2]

Finally, unlike animal domesticates and bonobos, humans can create cumulative cultures (Mesoudi, 2011; Laland, 2017). The cultural learning involved depends on enhanced attention to the actions of others, and this may explain the depigmentation of the sclera in humans, which Tomasello et al. (2007) suggested had evolved to facilitate gaze-following. Uniquely human forms of communication, engagement, and material technologies point to a cognitive and emotional profile that goes well beyond the

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[2] The observation that modern humans and wolves do not share variations in recently selected human genes (Theofanopoulou et al., 2017) is not surprising given the recent origin of these genes in humans and the far more ancient origin of wolves, which seem to have diverged from the highly social and cooperative coyotes 1.5 million years ago and apparently have not undergone intense social evolution since then.

reduced aggression shown in bonobos. The increased emotional plasticity of humans allows the modulation of emotional reactions on the basis of social situations and expectations: a norm-sensitive emotional control.

We believe that incorporating selection for emotional control and plasticity can better account for human behavior, affect and cognition, than selection for reduced aggression or pro-sociality alone. It can also explain why some traits are shared with domesticates, and others are not. The HPA axis, which affects fear and flight reactions in all vertebrates, is also involved in learning and memory (Sandi and Pinelo-Nava, 2007), so it is likely that mutations and epimutations in this system, and even more so in its regulation by higher cortical regions (which are involved in executive control) will be found in social mammals including bonobos and humans.

Selection for emotional control could account for the continued increase rather than decrease in brain size for most of human evolution. A study of self-control in 36 species of mammals and birds found higher levels of control to be best predicted by absolute brain volume, while also being correlated with dietary breadth in primates (MacLean et al., 2014). There are several brain regions (subcortical, cortical and neocortical) implicated in emotional control. These include the cerebellum, which is more broadly involved with attentional control and social skill-sets Schmahmann (2019), and prefrontal cortical regions that interact with the anterior cingulate cortex to form the executive attention network, which is critical for supporting the development of emotional regulation (Posner and Fan, 2008). Braunstein et al. (2017) pointed to four control systems that have been strongly implicated in implicit and explicit regulation of the emotions: the dorso-lateral prefrontal cortex (dlPFC), which is involved in subjective awareness, cognitive appraisal and strategic control (Lapate, 2018); the ventrolateral prefrontal cortex (vlPFC), which is implicated in the selection of goals; and the dorsal anterior cingulate cortex (dACC) and dorsal medial prefrontal cortex (dmPFC), which are involved in monitoring the compatibility or conflict between intended and actual behavioral outcomes and one's emotional states. In addition, the posterior parietal cortex (PPC) interacts with the dlPFC, exerts top–down, volitional control over attention and working memory processes, and supports perspective taking and spatial processing. Importantly, the PPC is strongly recruited during reappraisal that involves emotional distancing, suggesting that it regulates perceptions of an emotional stimulus' relevance or proximity (Silvers and Moreira, 2019). A recent phylogenetic analysis has found that disproportional increases in the volumes of the neocortex and the cerebellum occurred, respectively, at the origins of haplorrhines and of the apes, and not predominantly during the rapid and directional brain evolution observed in hominins. However, the general increase in brain size in humans means that these emotion-related brain regions are nevertheless larger than expected for a primate of similar body mass (Miller et al., 2019). We therefore suggest that the genetic and epigenetic networks underlying the development of these neocortical regions were major targets of selection during human social evolution, and that reduced aggression might be a symptom of broader social plasticity and more nuanced social emotions.

Advocates of HSD may argue that selection for emotional control and plasticity is not entirely distinct from selection against reactive aggression. However, the former is expected to be fundamental to the evolution of social motivation in many highly social animals and does not necessarily lead to a decrease in overall aggression; it is expected to lead to increased aggression in some social contexts and to increased cooperative behaviors in others – patterns of behavior than are seen in wolves and social mongooses. Since selection for emotional control is likely to involve both the early and late developmental pathways that underlie neural development, and since changes in the early pathways have multiple pleiotropic effects, it is to be expected that the behavioral, social and morphological evolution of social vertebrates will be affected by selection for changes in these pathways. Mutations affecting neural crest cells are therefore expected to be associated with several different aspects of social evolution, not just with domestication. We therefore do not find the notion of human self-domestication useful, and believe that the partial analogy with domesticates focuses too much on the reduction of reactive aggression and too little on social organization. With respect to cooperation, selection for emotional control in hominins was essential for alloparental care, cooperative hunting and foraging, and the improvement of lithic technologies, all of which had advantages that compensated for the higher metabolic costs involved with the increase in brain size and connectivity that is required for improved emotional and executive control. With respect to aggression, selection for emotional control better explains the extraordinary range of human violence: humans are far less impulsive than other apes, can better control their aggression in some social conditions, and are able to amplify their aggression in other conditions, leading to extreme cruelty. As we argue below the social-cognitive emotional profile of humans, whose underlying developmental pathways lead to the emergence of traits that partially overlap those that characterize the DS, is the consequence of selection for greatly enhanced emotional control and plasticity, which were linked with the culture-guided evolution of human capacities.

HUMAN SOCIAL EVOLUTION

Social Emotions and Emotional Plasticity in Pre-linguistic Humans

Early human evolution was marked by three novel and increasingly important behaviors: the production of stone tools (Laland, 2017), the consumption of meat and marrow (Ferraro et al., 2013; Thompson et al., 2019), and, somewhat later, the emergence of alloparenting (Hrdy, 2009). All bear an interesting relation to emotional control, pro-sociality and communication.

The use of sharp-edged stones for flesh removal and marrow extraction is found as early as 3.4 Mya (McPherron et al., 2010). Lithic traditions increased in complexity over time, demanding that individuals not only have the ability to comprehend long, hierarchical sequences, but also have the patience and tenacity to work through them (Pargeter et al., 2019). A knapper attempting to produce a complex tool (e.g., an Acheulian biface) has to keep various sub-goals constantly in mind, and to decide the manner in which he should proceed on the basis of the result of each flake removal. Both emotional and executive control are therefore necessary for the production of a complex stone tool (Stout et al., 2015). As for the social transmission of the skills and knowledge involved, ethnographic and experimental evidence both suggest that it requires flexible and creative mimetic communication and a high degree of pro-social motivation (Shilton, 2019). Experts and novices need to spend plenty of time together, to share a common goal of successful tool production, and to use their gestural communication for the purpose of teaching (Laland, 2017). Through joint knapping interactions, novices learn to see the core as the expert does, and become aware of the various visual cues that guide the next striking action (e.g., striking platforms, step fractures and grain quality). In other words, experts and novices need to establish a common ground based on communicative signals, which many researchers consider to be the starting point of human-specific communication (Tomasello, 2008). The benefits of better stone tools would therefore have promoted emotional control and plasticity, both for patient tool production, and to facilitate the kind of cooperative interactions skill transmission required.

Hunting and foraging skills also became increasingly more advanced during human evolution and, like tool-making skills, relied on cooperative activity and social learning. Even the more conservative scholars in the hunting vs. scavenging debate agree that by 1.5–1.0 Mya hunting was a regular component of hominin subsistence (Domínguez-Rodrigo and Pickering, 2017). The regular consumption of highly nutritious meat, fat and marrow answered the metabolic demands of larger brains. Since brain size is hypothesized to be related to self-control (MacLean et al., 2014), and since such control would improve the motor learning and social learning abilities of hominins (which, in turn, require even more self-control), a positive feedback loop might have been initiated at some point in human evolutionary history (see also Hare, 2017).

A large item of prey that was consumed by many individuals required communicating about it, moving it, guarding it, gathering around it, and eating it together without too many squabbles. It has been suggested that the hunting of megafauna, evident since approximately 1.7 Mya, indicates a concurrent and mutually reinforcing increase in group size and increased cooperative practices (Domínguez-Rodrigo and Pickering, 2017). The nature of plant consumption is more difficult to ascertain archaeologically, but studies in the ∼800,000 years old Acheulian site of Gesher Benot Ya'aqov provide evidence for the consumption of diverse plant species, mainly USOs (underground storage organs) and nuts. The extraction and preparation of these require complex procedures (Melamed et al., 2016) and, as in the case of tool-making, hunting and foraging skills, they were executed and socially transmitted through collaborative efforts in which visual cues in the environment needed to be mutually identified and responded to. USOs, for example, sometimes leave just small traces above ground, and digging implements are needed to retrieve the deeper ones (Thomas, 2006). Tracking, which is essential for hunting, involves recognizing spoors to infer the prey's location and physical state (Liebenberg, 2013). Selection for these skills involved selection for the emotional disposition and communicative abilities that they require.

Emotional control and pro-sociality were also likely to have been substantially influenced by alloparenting – the care of young by individuals other than their mother. Extensive alloparenting is universal in human societies (Sear and Mace, 2008), and among the great apes unique to humans (Hrdy, 2009). This practice has a proven impact on several other factors distinguishing human evolution and psychology, such as intersubjective abilities, proactive pro-sociality, brain size and altriciality (Hrdy, 2009, 2016; Isler and van Schaik, 2012; Burkart et al., 2014). Alloparenting may have emerged quite early in the hominin line because (i) cooperative breeding is especially likely to evolve in ecologically unstable environments (Hrdy, 2016); (ii) Australopithecus females were estimated to have given birth to babies who were more than 5% of their adult body mass compared to 3% in chimpanzees and 6% in modern humans (DeSilva, 2011); and (iii) there is evidence for extended altriciality in *Homo erectus* (Cofran and DeSilva, 2015). Strong trust relationships have to be formed in order for mothers to allow others access to their young: chimpanzee mothers, for example, are highly protective. Alloparenting may have developed in ecological conditions that kept mothers in close proximity to their familiar and trusted matrilineal kin. Allowing males and less related kin to provision and provide care is indicative of very high levels of group trust and tolerance.

The impact of alloparenting on human psychology is far-reaching, both for caregivers and infants. Fathers show increased oxytocin and decreased testosterone levels compared to non-fathers (Rilling and Mascaro, 2017), and caregivers' parenting behavior is correlated with distinct brain activation patterns, including circuitries that support, among other things, emotional empathy, comprehension of others' intentions and feelings, reward and motivation, and anxiety (Glasper et al., 2019). These appear to result in structural changes to the brain during parenting, such as an increase in both mothers and fathers in gray matter volume in the hypothalamus, amygdala and striatum (Kim et al., 2014; Kim, 2016). The prolonged brain maturation of human infants means a prolonged influence of postnatal environmental and social interactions on neural connectivity (Sakai et al., 2011; Miller et al., 2012). Compared to chimpanzees, human infants also show a more rapid increase in white matter volume in the prefrontal cortex, a difference that is probably related to social interactions (Sakai et al., 2011). Hrdy (2016) contrasts this with the much slower maturation of other brain areas, especially those related to motor coordination and mobility, and suggests that it can be partially explained by the greater importance for human infants of assessing the intentions and commitment levels of caregivers and of soliciting care.

All of the cooperative behaviors we have described both increased the adaptive value of emotional control and contributed to the extended pro-sociality of hominins. A life-style based on toolmaking, hunting, foraging, and alloparenting meant that early hominins were uniquely codependent and other-regarding compared to other great apes. The growing importance of cooperative alliances demanded a greater sensitivity to the expectations of others, which led to the emergence of social emotions like embarrassment, shame, guilt and pride, all signaled by the uniquely human blush (Crozier, 2006). The emergence of most of these self-evaluating emotions in development is thought to occur in the second phase of emotion regulation, during which children in their third to sixth year of life become capable of an intrapersonal regulation of their emotional actions and reflections (Holodynski and Friedlmeier, 2006).

Mimesis, Musical Engagement and Emotional Control

The method most likely to accommodate hominins' new cooperative behaviors is mimetic communication, or mimesis. Described initially by Donald (1991), the tool-kit of mimesis includes manual and bodily gestures (including the all-important gesture of pointing), facial expressions and vocalizations, mimicking, pantomime, and early musicking. The entire tool-kit involves multiple modalities, and represents the goals of individuals and collectives but, unlike language, it is not arbitrary and compositional, and is functionally limited to the here-and-now of the communication event. It allows for explicit cooperation at all the relevant levels, from information exchange, through explicit teaching of manual skills (in tool-making, hunting etc.), all the way to the maintenance of social life (through both micro-interactions and collective rituals). The implications of mimetic communication for the vocal modality in particular are far-reaching. Better executive control would have improved vocal learning abilities in humans, increasing the repertoire of vocalizations and making their use more flexible.

An additional factor affecting vocal flexibility is the relaxation of selection. Studies comparing the birdsong of white rumped munia to that of its domesticated strain, the Bengalese finch, show that relaxed selective conditions enable vocal learning that is less constrained than that observed in the wild and eventually leads to more complex songs (Okanoya, 2015). This implies that, in addition to the benefits of improved executive control, extended juvenile periods and more buffered human habitats may have also increased the variability and complexity of human vocal communication. A flexible and extensive use of vocal communication in the lives of hominins would have set the stage for the elaboration of the vocal modality in musical engagement and language.

We agree with Donald that mimetic communication and mimetic cognition are sufficient to account for the undoubtedly rich, yet in other senses limited, Acheulian cultural complex (Shilton, 2017). Although the skills and knowledge required for producing Acheulian stone tools and hunting megafauna are impressive, their social transmission is dependent mostly on cooperative interactions in the here-and-now, and do not require the extended functionality of language (described in the following section). As previously mentioned, the social transmission of both tool-making and foraging skills requires that skilled individuals share with novices their way of looking at and responding to the environment. Recognizing visual cues is essential for skills such as finding suitable raw materials for tools, identifying a good striking platform on a core, spotting the spoors of prey and predators, and locating underground storage organs. Mimetic communication would have enabled hominins to coordinate the way they perceived and engaged with the environment they experienced together – to reduce what Dor (2015) calls "experiential gaps," the inescapable differences in the way different individuals experience their surroundings. Mimetic communication, along with social motivation and theory of mind, can enable ensuing processes of what Dor calls "experiential mutual identification," in which hominins direct the attention of their counterparts to elements of interest in their immediate environment, attempt to share their attitudes toward them, and construct a mutually-identified collective view of the environment. This results in the creation of an intersubjective common ground, enabling flexible coordination within the here-and-now. By continually engaging in experiential mutual identification, hominins could transmit the diverse knowledge and skills they were continually acquiring. Hominin codependence would create a new evolutionary spiral in which new cooperative behaviors would continuously require upgrades to the toolkit of mimetic communication, the upgrades would enable new cooperative behaviors, which would increase codependence, and so on – an ever extending spiral of positive feedbacks, one in which humans may be said to be caught up in to this very day.

We believe that musicking played a crucial role in this process. Much has been written on the importance of music in human evolution, and we can address this literature only briefly (for a more thorough discussion, see Cross, 2007). It was discussed by Darwin (1871), who suggested musical behavior, grounded in the vocal expression of emotions and operating in the context of mating and sexual selection, was a precursor of language. After several decades of relative silence on the subject, interest revived in the 1990s, and was reinvigorated by Pinker's (1997) provocative and arguably ethnocentric claim that music is an "auditory cheesecake." This claim, which was based mainly on Western habits of passive music consumption, ignored the fact that in most of human history and for most human cultures musicking was and remains a participatory and highly social activity. Mithen (2006), who contributed substantially to the discussion, described musicality as part of the mimetic toolkit and envisioned a role for it in prehistoric lives.

We agree that musicking is mimetic in essence, but also think that some of its unique qualities merit a separate discussion and special recognition. One such quality is its anticipatory nature. Music contains tonal and rhythmic elements which are meant to trigger an embodied anticipation of its continuation. This anticipation relies mainly on rhythmic entrainment and repetition. Rhythmic entrainment, or beat-based timing, differs from interval-based timing (which has been documented for some primates) in that movements anticipate the onset of the musical beat, rather than merely corresponding roughly to the musical beat period (Merchant and Honing, 2014). Repetition is a universal quality of music (Nettl, 1983) and can even endow speech and random tone sequences with a perceived sense of musicality (Deutsch et al., 2011; Margulis and Simchy-Gross, 2016). Most importantly, repetition triggers more forcibly the anticipation of the next beat or sound. By supplying an anticipatory tonal and rhythmic foundation for play interactions and group mimetic acts, musicking substantially extends the potential for creating emotional synchrony and rituals of social bonding. Musicking is different from other forms of mimetic communication (as well as from language) because it establishes simultaneous rather than asynchronous interactions (Cross, 2016), as well as carrying highly embodied and ambivalent meanings (Langer, 1957; Cross and Tolbert, 2016). Musicking, unlike language, enables big groups to express themselves together; and while language excels at displacement, musicking is unusually potent in synchronizing the embodied experiences of participants, and with it, their arousal and emotional states.

We consequently suggest that musicking is a technology of engagement: communicative messages that are designed to strongly compel the receiver to emulate their rhythm and tonality. Music perception reflects this anticipatory nature of musicking by being highly embodied, predictive and, in a sense, inherently active. Beat perception, for example, is defined by the ability to predict the next beat, and engages motor areas of the brain regardless of any overt movement (Patel and Iversen, 2014). Listening to melodies similarly involves making involuntary predictions about their continuation (Margulis, 2005). Since there are non-arbitrary relationships between tempo, pitch, timbre and certain emotional states (Juslin and Laukka, 2003), and since emotional contagion based on automatic bodily mimicry results in emotional convergence (Hatfield et al., 1994), musical synchrony necessarily translates into emotional synchrony. This makes musical engagement a potent tool for emotionally uniting humans and for enhancing group cohesion and trust, which is particularly important during cooperative activities like hunting big animals or fighting with rival groups. As Darwin (1871) noted, social cohesion and solidarity would have a strong selective value at the group level.

While several species are capable of rhythmic entrainment, so far only parrots have been shown to respond to music spontaneously and with diverse movements (Keehn et al., 2019). This has led Keehn et al. (2019) to suggest five traits that are necessary for rhythmic entrainment: complex vocal learning, a capacity for imitation, an ability to learn complex action sequences, a tendency to form social bonds, and attentiveness to communicative movements. Wilson and Cook (2016) argue that what distinguishes parrots from other animals are two critical factors: social motivation and voluntary motor control. If so, it suggests that selection for executive control and pro-sociality would have made hominins responsive to rhythmic stimuli. But whereas parrots spontaneously respond to music with diverse movements, they do not *make* music. For hominins to create and develop this new form of communication, two other abilities were needed. First, proficiency in mimetic communication, which enables the flexible and intentional production of iconic bodily signals in a cooperative context; and second, the ability to create and sustain cumulative cultures, thus forming increasingly complex traditions of rhythmic and tonal group engagement.

Although it is difficult to establish whether musical engagement was directly or indirectly selected when it first appeared, it seems that the ability to engage in musical interactions is strongly related to other traits that are likely to provide fitness benefits, such as improved vocal and motor control, pro-social motivation, as well as good social skills and empathy (Keller et al., 2014; Novembre et al., 2019). Musical engagement could initially have evolved as a particularly engaging form of play and social grooming that was based on synchronous tapping, vocalizations and movements. Based on the ethnography of contemporary African hunter-gatherers, Lewis (personal communication) suggests that the first critical role of musical engagement was in deterring nocturnal predators. In time, musical engagement began to play a significant role in many other aspects of social life. Music's unique properties make it the only form of communication which allows several individuals to express themselves simultaneously as a single group, thus contributing substantially to social bonding, acculturation and the creation of group identity (Lewis, 2016). These contributions were probably adaptive at both the group level (more cohesive groups were more successful than less cohesive ones) and at the individual level (individuals who participate in musicking were trusted more than those who did not).

Studies on the neurochemistry of music point to its influence on factors related to reducing stress and enhancing social bonding (Chanda and Levitin, 2013). A meta-analysis of music therapy studies concluded that it is effective in reducing pain and anxiety (Kühlmann et al., 2018), something which appears to be related to reducing levels of cortisol and ACTH (adrenocorticotropic hormone). Listening to soothing music was found to increase oxytocin levels during post-surgery bed rest (Nilsson, 2009), and Kreutz (2014) found that, compared to dyadic chatting, group singing increased oxytocin levels, as well as significantly enhancing perceived psychological well-being. The pleasure derived from listening to music appears to be modulated by dopaminergic reward systems (Ferreri et al., 2019), and a PET study documented dopamine release in striatal regions during both peak arousal and in anticipation of it (Salimpoor et al., 2011). Tarr et al. (2014) also mention the likely influence of musical engagement on the endogenous opioid system, with exertion-related release of endorphins during musicking promoting social bonding.

Whatever the neurochemical mechanism, the influence of music on social bonding is well documented. Several studies have shown that movement synchrony alone promotes pro-sociality (Cirelli, 2018), with some finding positive effects on peer cooperation (e.g., Rabinowitch and Meltzoff, 2017). Reviewing the interpersonal effects of movement synchrony, Cross et al. (2019) highlight deindividuation, where the sense of self is diluted and one comes to feel less separate from others. The general effects of movement synchrony therefore provide the basis for collective emotions, which are intensified by the wide range of feelings embodied and induced through musical engagement, and by the creation of musical traditions unique to specific social groups.

Because musical interactions are based on the synchrony of embodied experiences, they can be a powerful tool for uniting a group in a single, socially mandated "mood," be it calm, joy, grief, anger (directed at another group) or ecstasy. Musicking continued to diversify alongside the emergence of language and more complex social structures, being utilized for a variety of social functions. Cross-culturally, musical engagement appears in broadly similar social practices, notably dance, ritual, religious ceremonies, processions, mourning, healing and infant care (Mehr et al., 2019). These diverse utilizations of musical communication in contexts that are critical for harmonious social life confirm its importance as a tool for modulating the emotions involved in collective activities and in responding to social demands. Musical engagement, made possible by a selection for emotional and executive control and pro-sociality, became a potent tool for promoting further pro-sociality, improving executive control, and inducing socially prescribed emotional states.

Language and Emotional Control

Mimesis could maintain the various cooperative behaviors we have described to a level that was probably sufficient for more than a million and half years. However, as codependency in hominin groups increased, it gradually required a system of communication that could break the boundaries of the here-and-now of the communication event, and allow the communication of experiences, norms, skills and worldviews beyond what was possible through mimesis. The new system of communication was language. It was built on the basis of mimesis, with the first prototypes of language appearing around a half a million years ago (Dediu and Levinson, 2013), and continued to evolve in a process of culturally driven, gene-culture coevolution until it acquired its fully fledged form (Dor and Jablonka, 2014).

All the tools of communication that we share with our ape relatives, and the toolkit of mimesis that is uniquely human, share a basic functional strategy: they enable communicators to target their interlocutors' senses, and present them with communicative materials to perceive. As Dor (2015) shows, the functional uniqueness of language lies in the fact that language abandons this strategy – it allows speakers to communicate directly with their interlocutors' imaginations. It permits speakers to intentionally and systematically instruct their interlocutors in the process of imagining the intended meaning instead of experiencing it. Speakers provide interlocutors with a code, a structured list of the basic co-ordinates of their experience, which the interlocutors then use as a scaffold for their own imagination. Following the code, the interlocutors raise past experiences from their own memories, and then reconstruct and recombine them to produce novel, imagined experiences. Language is thus the only system that allows the communication of meanings that cannot be presented to the senses. This includes experiences from the past and from other places (this is Hockett's displacement: reference to things remote or "displaced" in time and space), but also, and as importantly, a very wide variety of inner experiences that are very difficult to present, even if they refer to the here-and-now. The fact that the communicator is worried, for example, may show itself on his or her face, but if the object of worry is not directly available for perception, it will remain uncommunicable without language. Language makes it communicable, and it does so on the basis of the collective effort of experiential mutual-identification that has already been established in the mimetic period. The crucial upgrade is that every point of experiential mutual-identification is symbolically marked by a mutually identified sign – lexical, morphological or syntactic. This symbolic signification allows speakers to translate what they want to communicate into formally arranged symbolic codes and transmit the codes to their interlocutors. The interlocutors analyze the codes, retrieve from their memories the relevant experiences that are associated with the signs, and construct their own imagined experiences.

Language thus revolutionized hominin life. For the first time, individuals could begin to take into account things they themselves have never experienced, things they only heard about. Communities could begin to explicitly negotiate collective conceptualizations of the world, norms of social conduct, and plans for future collaborative activities, all of which in the mimetic period could only be implicitly and indirectly negotiated through perceptible behavior (Dor, 2019). Stories (both factual and fictional) became a crucial mode of information transfer, identity synchronization and negotiation of social behavior and norms (Smith et al., 2017; Boyd, 2018), and conversations allowed explicit complaints and criticism (Wiessner, 2014).

As we see it, once in place, the evolution of language must have entailed profound alterations to hominins' emotional profiles and in their capacities for emotional control. At the most foundational level, the emergence of a linguistic communication technology that transcends individuals' immediate experiences of the here-and-now required them to develop increasing levels of trust and the control of affect-related drives and triggers of action. When told about things beyond what they could perceive by themselves, whether dangerous or beneficial to them, individuals had to imagine those things while either inhibiting, modulating or mobilizing the appropriate emotional response. They also had to face new problems: they needed to reduce the dangers of false memories and distinguish between what they recalled on the basis of their own experiences and what they recalled on the basis of stories told by others. These dynamics led, among other things, to the evolution of the human-specific phenomenon of distinguishing between thought and feeling (Jablonka et al., 2012).

The instruction of imagination, which is what language enables, has another problematic aspect: it revolutionized deception and enabled the uniquely human phenomenon of the lie. Many evolutionary-oriented scholars argue that this new capacity for lying was a major obstacle to the emergence and stabilization of language itself (Boyd et al., 2003; Knight, 2007; Mercier and Sperber, 2011; Tomasello, 2016). Their argument is based on the idea that linguistic communication requires trust: if everybody lies to everybody else, the trust breaks down, and language itself follows suit. As Dor (2017) shows, however, this line of reasoning is based on a series of unrealistic assumptions. It concentrates on a single type of lying, where an individual lies with an explicit exploitative intention, and the lying carries real detrimental consequences for the community, but this is far from representing the functions of lying in linguistic communication. Individuals very often lie with non-exploitative intentions, sometimes with pro-social intentions ('white lies'), and such lying actually contributes to social cohesion. Potentially detrimental and exploitative lies are effectively policed and punished in small groups, so exploitative lying is unlikely to destroy linguistic communication. Moreover, language is not restricted to the transfer of propositional information. It is necessary for collective action and collective identity, so the multiple functions of language compensated for its occasional and inevitable detrimental effects. Especially relevant to our current discussion is the fact that lying, both exploitative and non-exploitative, requires more sophisticated capacities at the cognitive, emotional and social levels, than honest communication. It did not harm the overall capacity of the community to cooperate, but made the social negotiation of community life more nuanced and broader in scope. Lying requires higher levels of emotional control of behavioral expressions – bodily, facial and vocal – than honest communication (Dor, 2017); efficient lying requires a poker face and the ability to express pretended emotions. Language, therefore, would have added to the selective pressures for better mimesis-related emotional control, rather than reducing the need for it. A similar dynamic would have occurred at the underlying physio-anatomical level of adapting to language, as the appearance of the modern vocal apparatus made the human face highly mobile and controllable, thus increasing the repertoire of facial expressions and their voluntary control (Donald, 1991; Wilkins, 2017). In addition, language was arguably able to provide its own means for emotional control, whether for lying or other purposes. Neuroimaging studies show that stimulus reappraisal, a widely acknowledged cognitive process of emotion regulation (Ertl et al., 2013), is correlated with activity in brain areas that are involved with the representation of semantic knowledge and its retrieval (Wagner et al., 2001; Satpute et al., 2014). Although semantic knowledge is not necessarily linguistic, its digitization and massive expansion during the emergence and development of language (Dor, 2015) could have allowed hominins living in linguistic groups to better categorize, appraise and reappraise emotion-provoking stimuli, and thus better control their responses to them.

In addition, the mutual identification, categorization and signification of emotional experiences led to the emergence of a semantic field of emotion – sets of semantically related words and expressions referring to mutually identified emotions. Emotion-words enable affect labeling, a language-specific technique of emotion regulation, which can modulate an emotional experience, its accompanying physiological response and the resulting behavior, in accordance with the emotion-word used for categorizing the initial affective response. For example, a stress response can be categorized by an emotion-word as either exciting or fearful, and this alters the resulting emotional experience, the physiological correlates and the behavioral responses of the individual that utters or responds to the emotion-word (Jamieson et al., 2013). Another possible contribution of emotion-words for emotional control is in their use as scaffolds for endogenous emotion generation, a process which in itself can be used to regulate emotional responses to external stimuli (Engen and Singer, 2018). For example, an emotion word such as "anger," when used in the context of a conflict with an out-group member, could help mobilize an aggressive response.

Hare (2017) cites evidence that the widening of the developmental window enables human children to reach, around age 6, levels of self-control that exceed those of non-human apes. It is around this same age that children begin to internalize means of emotion regulation including speech signs, so audible taunts and curses become silent ones, a visible smile becomes an inner smile, and on the linguistic level, audible speech becomes inner speech (Holodynski and Friedlmeier, 2006). Symbolic strategies are increasingly employed by caregivers to instruct the children under their care, teaching the children why and how they should control and express their emotions (Holodynski and Friedlmeier, 2006). Such a dynamic puts the individual child's unique emotional profile and its expression under collective pressure, making him comply with shared cultural norms and reflect on his emotional state and its regulation.

The emergence of language in hominin evolution added to shared cultural norms a gradually increasing subset of language-specific norms of communication, such as conventionalized conversational styles. This would have placed additional selective pressures on individuals' capacities for emotional control. Living among egalitarian, coordinated groups requires a heightened sensitivity to the motives and emotional states of others, especially while negotiating smooth interactions between group members. As data from modern hunter-gatherer societies show, these requirements may result in pervasive conversational styles of surface courtesy, which are achieved through a conspicuous and conventionalized politeness (Brown, 2004; Groark, 2008). The effects of these or other norms of linguistic communication on the emotional lives of their speakers may vary according to how different linguistic groups (and different group members within them) view the relations between language and experience (Dor, 2015). For example, in Tenejapa Mayans, conspicuous politeness, which includes politeness utterances, serves to convey agreement, empathy, and positive affect (Brown, 2004), thereby promoting pro-sociality. In Tzotzil Mayans, on the other hand, aggression has been transferred from the physical level (assaults and murders are relatively uncommon) to the symbolic-linguistic level. Ill-wishing utterances are believed to possess a sorcerous quality when uttered within the privacy of one's residency, often during the night, i.e., away from everyday social interaction and its linguistic norms of politeness (Groark, 2008).[3]

Language has also led to the cultural construction of novel categories of feelings (or emotions; we use the terms interchangeably here). For example, feelings of certainty,

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[3] The symbolic norms regulating human behavior, which are culturally learned and culturally evolved, make it possible to argue that humans are "domesticated" by externally imposed symbolic social conventions (and by an internally constructed, norm-binding "super-ego"). This notion of HSD, which goes back to the old and misleading idea of humans being tamed by "civilization," is very different from the current one. Moreover, the regulation of human life by symbolic norms and conventions has little in common with the taming of domesticates, or with the social evolution of bonobos and other social mammals.

suspicion and doubt derive from issues of truth and falsity as properties of the relationship between a linguistic message – arbitrary and displaced – and the experiential world (Jablonka et al., 2012). Other existing, prelinguistic feelings came to be mutually identified and reconceptualized in ways that align with the values, myths and the shared worldview of a linguistic group's semantic landscape. As Myers (1988) shows in his conceptual analysis of 'compassion' and 'anger' in the culture and language of Pintupi Aborigines, these emotion-words refer to the acceptance or rejection of relatedness. "Compassion" refers to the acceptance of relatedness and "anger" to its rejection. Generally, once people construct overall shared worldviews through language and myth, their linguistic emotion-concepts will come to reflect this "deep structure."

At the simplest level, the sharing of experiences through language has allowed individuals to expand their private experiential knowledge, including emotional knowledge (Jablonka and Ginsburg, 2012). This sharing of emotional knowledge could have been achieved by the use of metonyms and metaphors (e.g., the "head" of the group; having the upper "hand"), which derive from the shared anatomy and physiological functioning of the human body and appear to be a universal tool for cultural-specific content (Kövecses, 2000). Linguistically constructed emotion concepts that are combined together further elaborate the semantic emotional knowledge of individuals (Barrett, 2017). They bring together diverse bodily sensations, thoughts, feelings, and social contexts in unique configurations.

CONCLUSION AND FUTURE DIRECTIONS

Domestication is the longest and the most systematic evolutionary experiment that humans have ever conducted. It was used by Darwin (1872) to explain evolutionary change through natural selection and assortative mating, and in the *Variation in Animals and Plants under Domestication* (Darwin, 1868) to shed light on the generation of heritable variations. It has profoundly changed the history of humans, being a necessary condition for the agricultural revolution (Diamond, 1997), and is used today as an example of evolutionary change that highlights the need to incorporate multiple modes of information transmission (genetic, epigenetic, behavioral and cultural) when considering cumulative evolution (Zeder, 2018). The social evolution of humans and bonobos has been interpreted as a special variant of domestication – as a self-domestication process. While this analogy has led to productive research because it focused attention on the commonalities of humans and domesticates, we believe that the social evolution of humans is better explained in terms of selection for pro-social motivation and self-control, which are guided by symbolic communication and representation rather than as a process of self-domestication.

In this paper we have emphasized the differences between the evolution of domesticates and the social evolution of humans. First, while in domesticates there is a breakdown of social structures (Spurway, 1955), social structures in humans became more complex. Second, in most domesticates there is a reduction in brain size whereas brain size increased during most of human evolution. It is possible that in humans the last 10,000 years of sedentary life led to small-island-like conditions, which could arguably explain the recent reduction in human brain size (Sánchez-Villagra et al., 2016). Generally, however, although selection for reduced emotional reactivity was involved in both socially impoverished domesticates and socially sophisticated humans, the differences between the two types of pro-social evolution mean that their inclusion under the same umbrella term of "domestication" is misleading.

Third, the evolution of all cooperative and sophisticated social animals, including humans, was inevitably entwined with changes in their emotional dispositions. We observe, on the one hand, context-sensitive reduced aggression and displays of affection toward some group members. Notable examples are teaching the young by non-parents in meerkats, alloparenting in wolves, and sophisticated, hierarchical social structure and reduced aggression of mole rats (Skulachev et al., 2017). On the other hand, in some of the same cooperative species we find increased aggression toward group members, mainly in the context of status-related conflicts. For example, the offspring of a subordinate meerkat females that have become pregnant are killed by the dominant female, and such subordinates are often evicted from the group; in addition, subordinates may engage in infanticide activities, though to a significantly lesser degree (Clutton-Brock et al., 1998). Proactive violence against other groups is also evident in meerkats and other cooperative species. What is striking about these and most other examples of social behavior in cooperative taxa is the increased context-sensitivity of both pro-social and aggressive behaviors, which points to an altered emotional responsiveness. We therefore expect that comparing humans with other social mammals will be as fruitful as comparing them to domesticates. We anticipate that future research will uncover similarities in the executive control of emotions among humans and other highly social mammals, which will only partially overlap the early developmental pathways that are affected in the DS. It would be of particular interest to study the correlations between neoteny, increase in brain size and alloparenting practices in humans and other highly social mammals, and compare the developmental networks that underlie these cooperative behaviors.

More specifically, we expect that the developmental pathways and the genetic and epigenetic networks underlying cooperative behavior, neoteny and other features related to pro-sociality in humans and other social mammals will include neural crest-related gene networks. These networks underpin cranial differences and other important morphological and physiological changes that are involved in domestication and have been targeted by selection during the social evolution of humans. However, we predict that in humans, changes in the GRNs underlying the HPA axis and pathways associated with learning and with the control of emotions, will be even more prominent. The nature of the changes in the cognition and emotionality of humans suggests that pathways controlling metacognition (e.g., complex decision-making and regulation of affect), which are controlled by neo-cortical regions, were important targets of selection. These pathways are also expected to underlie the social evolution of other mammals that became socially organized and cooperative with regard to tasks such as foraging, hunting, group defense and alloparenting. Hence we predict that genetic and epigenetic changes in the GRNs underlying the development of these pathways will prove to be of major importance in the evolution of highly social mammals and to be especially prominent in human evolution.

Extending Hare's (2017) suggestion, we have argued that the evolution of emotional self-control is the hallmark of human social evolution, and that self-control is part of the cognitive-affective evolved make-up of humans. We identified two overlapping stages in the process, one preceding the emergence of language and the second following it. The first stage involved the initial development of the hominin life-style: hunting and foraging, toolmaking, and alloparenting. Each of these practices both profited from and promoted an increase in emotional control and pro-sociality. As argued elsewhere (Dor and Jablonka, 2010, 2014; Dor, 2015), the evolution of all forms of uniquely human communication – including mimesis, musical engagement and language – was driven by cultural evolution. (For extensive discussion of human cultural evolution see Richerson and Boyd, 2005; Mesoudi, 2011; Jablonka and Lamb, 2014; Henrich, 2016; Laland, 2017.) The evolution of human communication was initiated by cultural practices that shaped the plastic human brain through learning-based adjustments, followed by the partial genetic accommodation of elements enabling ever more complex communication. Hence, culturally evolved communication not only adapted to the brains and minds of individual communicators, but the brains and minds of the communicators became adapted to the culturally evolving communication systems, thereby generating, through positive feedbacks, an ever-widening co-evolutionary spiral. We have argued that the evolution of pro-sociality and cooperation in pre-linguistic humans was a major part of this spiraling evolutionary process. Among other things, it entailed the evolution of increased emotional control and mimetic communication, including rhythmically entrained mimetic acts that are the seed of musical engagement. Building on the foundation of rhythmic and tonal anticipation, musical activities became a powerful technology of engagement, capable of inducing high levels of emotional synchrony and promoting pro-social behavior. Because of this, we expect to find that limbic regions involved in emotional reactions became specialized during human evolution, as were the neo-cortical regions controlling them (for some indications that this may indeed be the case, see Barger et al., 2014.) According to our argument, the basic social emotions of embarrassment, shame, guilt and pride evolved in this context. We expect that once the developmental genetic networks underlying them (and the blush, which is their outward expression) are identified, the relevant variations will be found to be shared by modern humans and their Neanderthal and Denisvoan cousins.

The second stage that we identified in human evolution involved a further increase in emotional and cognitive plasticity that was driven by the instruction of imagination through language. We therefore expect, and find, a strong cultural influence on the expression of emotions, including the ability to suppress emotions under some social and intellectual conditions. We also expect, and find, that the new adaptations in the ability of humans to represent and to communicate have led to a huge increase in the ability to deceive and to the problem of distinguishing between false and true memories, problems that were partially solved by cultural evolution of social norms and the development of autobiographical memory (Jablonka, 2017; Dor, 2019). More culture-specific changes in the control and effects of emotions can also be explained within this framework. Sapolsky (1999), for example, discusses the case of individuals with repressive personalities whose "unemotional" lives of discipline and conformity are actually characterized by markedly elevated basal cortisol levels and hyper-reactive sympathetic stress-responses. These findings are notable because repressive personalities are not exposed to irregular amounts of stress with which they are coping maladaptively, but rather are highly stressed by the process of constructing a world without any stressors. We see this case as illustrative of the ways in which human-specific emotional control and emotional plasticity, mediated by language and other uniquely human cultural practices, may modulate and mold human physiology, and in doing so lead to a phenotype that partially resembles that of domesticates.

In summary, we regard the social, gene-cultural evolution of humans as more similar to the social evolution of other highly social mammals that display enhanced cognitive and affective plasticity and sophisticated social structures, than to the evolution of socially impoverished domesticates. These similarities however, pale in comparison to the unique features of human social evolution, which has been guided by cumulative cultural changes that led to increased cognitive and affective plasticity, allowing feats of saintly cooperation and sadistic cruelty that go far beyond those of any other animal.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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