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CHAPTER

Self-domestication and the Cultural Evolution of Language

Limor Raviv, Simon Kirby

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Abstract

The structural design features of human language emerge in the process of cultural evolution, shaping languages over the course of communication, learning, and transmission. What role does this leave biological evolution? This chapter highlights the biological bases and preconditions that underlie the particular type of prosocial behaviours and cognitive inference abilities that are required for languages to emerge via cultural evolution to begin with. Specifically, the human self-domestication hypothesis was invoked to explain the evolution of modern humans, suggesting that many of humans' distinctive traits—including language—are the result of an evolutionary process similar to that of animal domestication. This chapter proposes that prominent changes in human behaviour and ecology associated with self-domestication may institute the forces that shape the cultural evolution of language by enriching the opportunities for learning and teaching and by promoting communication and cooperation.

Keywords: language evolution, human evolution, self-domestication, teaching, prosocial behaviour, play,

communication, learning

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Introduction: The Origin of Language Structure

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Language is one of the hallmarks of human cognition and is considered unparalleled by any other animal communication system. Its uniqueness lies in its seemingly unlimited expressive power, which is enabled by a set of rule-like grammatical structures. One of the principal explanatory goals for linguistics and cognitive science is thus to understand *why* languages have the structure they do, and where these structures come from.

Lab experiments and computational models over the past 20 years suggests that many of the universal properties of language are the result of a trade-off between two partially competing pressures that operate

on languages in the process of cultural evolution: a pressure for *compressibility* and a pressure for *informativeness* (e.g. Kirby et al., 2015; for review see Bailes & Cuskley's chapter, this volume). Specifically, the pressure for compressibility seems to arise from learning and constraints on memory, while the pressure for informativeness seems to arise from communication and the need to differentiate between different meanings, with experimental and modelling work demonstrating that neither alone is sufficient (e.g. Kirby et al., 2015; Motamedi et al., 2019, 2021; Raviv et al., 2019; Winters et al., 2015).

In the context of cultural evolution of language, learning is defined as a process whereby an individual acquires their language (or any other target behaviour for that matter) by observing the linguistic behaviour of others in their community, be it their peers (i.e. horizontal transmission) or their parents (i.e. crossgenerational transmission). This process involves inductive inference, where learners must infer the language(s) of the set of signals produced by individuals around them, despite the fact that these signal sets are inevitably only a subset of their full linguistic knowledge/abilities (i.e. we can never produce the entire set of possible signals in the language) (Kirby, 2002; Zuidema, 2003). This is why more compressible languages are preferred: compressibility has been argued to be a universal prior for inductive inference (Chater & Vitányi, 2003; Culbertson & Kirby, 2016), meaning learners have a prior expectation that languages will take the form of sets of generalizable linguistic rules rather than unstructured lists of unconnected facts. Another aspect of cultural evolution is communication, in which language users rationally produce signals that direct their interlocutor to a particular meaning of interest, and where receivers of these signals infer these meanings from a set of possible meanings. This process thus also involves inference, although note that this inference is not about languages per se but rather about the mental states and/or intentions of those with whom an individual is communicating. This view of the cultural evolution of language provides us with two clear prerequisites for the origins of linguistic structure: an ability to inductively infer the system of signals in their language, and also an ability to infer the mental states and communicative intentions of other language users.

The Biological Bases for the Cultural Evolution of Language

The important role for cultural evolution in explaining the origins of the fundamental structural properties of language does not diminish the importance of biological evolution in explaining the origins of language. Indeed, there must be something that leads humans and no other species to exhibit a communication system with the particular and unique properties that languages have. But rather than biological evolution giving rise to language structure directly, instead we argue that biological evolution must have given rise to the specific mechanisms outlined above that enable culture evolution in our species, namely, our ability to *learn sets of signals*, and our ability to *infer communicative intentions*.

In the following section, we will advocate a prominent approach to understanding human evolution, namely, the human self-domestication (HSD) hypothesis, which suggests that many of the features that make humans unique are the outcome of an evolutionary process similar to that of animal domestication (Benítez-Burraco et al., 2020; Hare, 2017). According to this evolutionary hypothesis, human self-domestication resulted in less aggressive individuals who were more prone to interact with others (particularly with their kins and in-group members, but also with strangers), leading to increased social contacts and community structure as well as more sophisticated forms of explicit teaching, learning, and exploration. Crucially, these properties may have ultimately given rise to the specific niche that enabled the cultural evolution of many distinctive human traits.

The human self-domestication hypothesis has also been invoked to explain the evolution of human language in particular, putting cultural evolution front and centre as an explanatory mechanism for shaping our linguistic abilities and tendencies (Benítez-Burraco, 2020; Benítez-Burraco et al., 2021; Benítez-

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Burraco & Kempe, 2018; Benítez-Burraco & Progovac, 2020; Langley et al., 2019; Progovac & Benítez-Burraco, 2019; Thomas & Kirby, 2018). Besides drawing on analogies with other domesticated animals who exhibit more rule-based communication systems than their non-domesticated relatives, the potential explanatory link between self-domestication and language evolution is motivated by the fact that many of the biological and cognitive changes which are at the very core of our linguistic abilities (and the process of cultural evolution itself) are brought about by self-domestication. We highlight the main theoretical arguments that stand at the heart of this proposal (see Language Evolution via HSD), focusing on the contribution of four specific and prominent features typically associated with self-domestication in humans: increased prosocial behaviour, buffered environment, extended juvenile period, and enhanced play. For each of these features, we demonstrate their potential causal role in shaping languages with respect to the two relevant aspects of cultural evolution outlined above: learning of signals, and enhanced communication.

The Human Self-Domestication (HSD) Hypothesis

Humans share many traits with domesticated animals, such as dogs, cats, pigs, and sheep. Specifically, anatomically modern humans exhibit many of the biological and behavioural characteristics that are typically associated with the outcome of a domestication process in other mammals—a set of features also referred to as the 'domestication syndrome' (Hare, 2017; Sánchez-Villagra et al., 2016; Wilkins et al., 2014; Zeder, 2012a, 2012b). These characteristics include, amongst others, biological and physical traits such as child-like facial features, reduced sexual dimorphism, extended juvenile period, and hair loss, as well as cognitive and behavioural traits such as enhanced social cognition and sensitivity to social cues, increased play behaviour, and reduced reactive aggression. The striking similarities between humans and other domesticates, which have been noted already in Darwin (1871), have led researchers to believe that humans may have also undergone an evolutionary process similar to that of animal domestication (Hare, 2017). But whereas animal domestication is directly and intentionally guided by humans via artificial selection for tameness, humans' self-domestication is suggested to have been an organic process, likely triggered by internal and non-directed pressures favouring prosocial behaviour over aggression (see the following paragraph and in the next section). Thus, self-domestication can effectively be seen as a sort of cultural niche construction, in which a species (in this case humans) reduces or redirects the impact of selective pressures that individuals experience via gene-culture coevolution (Laland et al., 2000).

The HSD hypothesis, which is most notably articulated in Hare (2017), suggests that human evolution in the middle and late palaeolithic was characterized by selective pressures for less aggressive sexual and social partners. Out of the many factors that were suggested to trigger this selection for less aggressive behaviours in humans, the two most prominent explanations are (i) changes in our foraging ecology, whereas humans began relying on cooking as well as non-local food sources, entailing the need to move around and share resources with others (Pisor & Surbeck, 2019), and (ii) climate deterioration and harsh environmental conditions during the last glaciation, which have increased the need for exchanging and/or sharing resources between groups (Spikins et al., 2021). In both cases, selection for intergroup tolerance and less aggressive individuals would have benefitted the survival of the entire population, and as such might have triggered the process of self-domestication in humans.

Effectively, the neural underpinnings of such reduced aggression and increased tolerance following HSD are likely to lie in evolutionary processes resulting in higher levels of serotonin and oxytocin in the brain (Agnvall et al., 2015; Cieri et al., 2014; De Dreu & Kret, 2016; Plyusnina et al., 1991), reduction in the production of testosterone (Eisenegger et al., 2011; Montoya et al., 2012; Wobber et al., 2013), socially regulated cortisol levels (Gunnar & Donzella, 2002; Wobber et al., 2010), and increased hippocampal neurogenesis (Huang et al., 2015). For instance, humans and other domesticated species typically exhibit elevated serotonin levels, which were shown to promote defensive (as opposed to offensive) behaviours in

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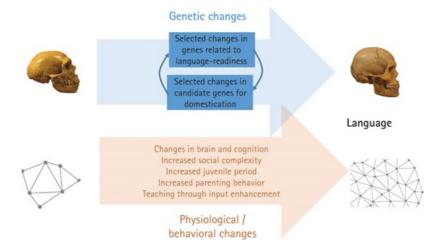
animals (Blanchard et al., 1998), to inhibit predatory aggression (Nikulina, 1991), and to promote more cooperative behaviours in humans (Wood et al., 2006). In addition, socially sensitive production of the hormone cortisol has been regarded as a confident biomarker of altered response to stress across species and across child development, with increased cortisol levels associated with physically and socially stressful conditions (Gunnar & Donzella, 2002; Montoya et al., 2012).

Interestingly, the selection against aggression in our species resulted not only in physiological changes typically associated with domestication (e.g. neoteny, smaller teeth, pigmentation) but also led to a set of crucial cognitive and behavioural changes. These changes include enhanced cooperation and social tolerance, playfulness, reduced in–group aggression, and consequently, more frequent and more elaborate connections with both kin and non–kin individuals, which characterize human's widespread social networks (Apicella et al., 2012; Hill et al., 2014; MacDonald et al., 2021). Together, the HSD hypothesis suggests that our self–domestication may be responsible for many of the hallmark traits of humanity, and specifically for many of the traits that distinguish humans from Neanderthals (Theofanopoulou et al., 2017).

Language Evolution via HSD

Out of the many possible outcomes of domestication, much emphasis has been placed on the enhanced communication and cooperation exhibited by domesticated animals, including humans. Notably, in our species, communication and cooperation are mostly achieved by one tool: language. As such, it is not surprising that self-domestication has been invoked to specifically explain the evolution of human languages (Benítez-Burraco, 2020; Benítez-Burraco et al., 2021; Benítez-Burraco & Kempe, 2018; Benítez-Burraco & Progovac, 2020; Langley et al., 2019; Progovac & Benítez-Burraco, 2019; Thomas & Kirby, 2018). In particular, it is argued that HSD fuelled the processes and cognitive abilities that underlie the cultural evolution of language to begin with (see Figure 1), and that it can help explain critical features of modern language such as pragmatics and turn-taking (Benítez-Burraco et al., 2021), grammar sophistication and innovation (Langley et al., 2019), child-directed speech (Benítez-Burraco & Kempe, 2018), and even cross-linguistic variability (Benítez-Burraco, 2020; Benítez-Burraco & Progovac, 2020).

Figure 1



The evolution of language under the effects of self-domestication;

Adapted with permission from Benítez-Burraco and Kempe (2018).

The story of how self-domestication might have shaped the evolution of language is illustrated in Figure 2 and starts with a general selection pressure in favour of more prosocial behaviour and reduced aggression.

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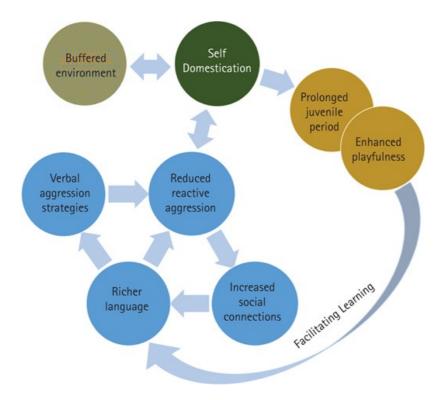
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While this initial selection pressure was likely triggered by external and internal factors such as harsher environments and changes in our foraging behaviours, these changes in aggression management also resulted in drastic changes to our social dynamics. Specifically, more tolerant individuals were able to establish stronger, denser, and more multiplex networks, consisting of kin and close in-group members who frequently interacted with each other about a range of social and environmental topics. In turn, these increased social connections required more informative and cognitively demanding languages to facilitate these complex interactions. But once these more informative languages were available, they again facilitated even more complex connections with even more people, and stimulated more prosocial behaviour—also towards strangers from more distant groups. As such, increased prosociality and language sophistication (in the sense of languages becoming more and more informative) can be seen as engaging in a sort of mutually reinforcing feedback loop, which is driven by the basic pressure for reduced aggression that underlies self-domestication (Figure 2) (Benítez-Burraco & Progovac, 2020; Progovac & Benítez-Burraco, 2019). Notably, as languages became more and more informative and rich, they also developed more rule-like compressible structures in the process of cultural evolution, which allows learners to derive a set of productive rules rather than memorizing all possible individual forms. In addition, it was suggested that reduced physical aggression and the rise of richer conversational strategies for expressing verbal aggression also created a positive feedback loop that reinforced self-domestication in our species. In essence, the idea is that reduced physical aggression gave rise to new forms of language, including the possibility to express verbal aggression by arguing and using insults and swearing. These forms of verbal aggression may have then replaced physical aggression altogether in some cases, and as such further reduced the levels of direct aggression between individuals—effectively accelerating the processes of selfdomestication yet again (Figure 2).

Crucially, self-domestication can reinforce the core mechanisms that are involved in the cultural evolution of languages, namely, communication and learning—which give rise to the pressures for informativeness and compressibility that drive the structure of language over time, as discussed above. For example, *reduced aggression and increased prosociality*, which are the most prominent traits of self-domestication, directly impact both communication and learning in profound ways. In the case of adults, reduced aggression enables longer, more frequent, and more elaborate contacts with both in–group and outgroup members, which clearly lie at the very heart of our enhanced communication behaviours—increasing the need for richer communicative inference and more elaborate and informative linguistic tools. In the case of children, more tolerance and social bonds have likely led to a significant increase in both the quality and quantity of child-adult interaction, which facilitate language learning of an increasingly growing set of signals. Here, contact with (and exposure to) larger and more diverse networks of caregivers can facilitate language acquisition by providing children with access to richer and more variable linguistic input—which is known to boost language learning and generalization (e.g. Clopper & Pisoni, 2004; Rost & McMurray, 2009; Seidl et al., 2014) as well as inference abilities (Heit & Hahn, 2001; Osherson et al., 1990).

Figure 2



An illustration of the feedback loop between reduced aggression, language evolution, and self-domestication outcomes.

Besides reduced aggression, the process of self-domestication entails other significant changes in our developmental trajectory and our surroundings, which also have the potential to impact the processes of learning and communication. Next, we focus on three other prominent markers of domestication across species: buffered environments, extended juvenile period, and enhanced play behaviours. Below we show that each of these features has the potential of shaping both learning and communication ecologies, and thus affect the cultural evolution of languages.

First, a typical marker of (self-)domestication is a kind of buffered environment, characterized by reduced exposure to predators and other hazards and more consistent and reliable food supply. This leads to less and/or weaker selection pressures typically associated with survival in the wild, and effectively relaxes the pressure for keeping signals relatively stereotypical and rigid—opening the door for more variability and flexibility to emerge (Deacon, 2010). This idea is supported by the finding that, in some species of birds such as the Bengalese finch, the process of domestication triggered an increase in song variation and innovation (Okanoya, 2017; see Thomas & Kirby, 2018 for a review). The Bengalese finch is a domesticated songbird bred in Japan for the past 250 year, and selected from its wild relative, the white-rumped munia, specifically for its white plumage. What makes the Bengalese finch so interesting is how, by comparison with the munia, its vocal learning behaviour has changed dramatically in the course of 250 years of selective breeding. Although both the munia and the Bengalese are vocal learners that acquire their repertoire of vocal signals over their lifetime through a process of production learning, the song of the Bengalese is considerably more variable, displaying a richness of syntactic structure not seen in the wild bird. In addition, the Bengalese finch is more flexible in its song: whereas munia chicks will tend to only learn a very narrow range of species-specific songs, the Bengalese finch is less constrained and able to learn a wider range of songs from multiple sources. Notably, the relative flexibility of Bengalese song was attributed to its domesticated environment, which buffered finches from a range of natural dangers, and led, over many generations, to a biological change in their stress response system (and specifically, reduced cortisol). With reduced stress and reduced constraints on receptivity to variation in input, the domesticated bird was more

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free to shift away from innate canalization of song behaviour towards social learning and the cultural evolution of song. In other words, signal enrichment can arise purely as a side-effect of domestication, which can ramp up song complexity through increased reliance on social learning (Ritchie & Kirby, 2005, 2006). Similarly, the buffered environment resulting from self-domestication might have contributed to the emergence of more informative and compressible forms of language in our species.

Note that in the Bengalese finch case, environmental buffering is externally created by the domesticator (the finch breeders), and this is part of the cause of domestication effects. However, we suggest that domestication (and particularly, self-domestication) also may itself create environmental buffering. This is perhaps seen most clearly in the products of human domestication, where our cultural products (that we argue arise ultimately from domestication) have themselves the effect of further buffering us from the environment. In this sense, domestication may create a feedback loop of reciprocal causation. Downstream effects of buffering, such as reduced aggression and increased social connections, may further buffer a species from environmental contingencies.

Another key outcome of domestication in a wide range of animals is an extended juvenile period (i.e. neoteny), which critically affects learning ecologies and affordances, and as such has likely contributed to shaping the cultural evolution of language (see Benítez-Burraco & Kempe, 2018; Langley et al., 2019 for detailed discussion). Specifically, a prolonged developmental window and prolonged childhood can impact learning in two ways. First, they give rise to more learning opportunities through culture, imitation, and exposure—as opposed to innate knowledge—which can in turn facilitate the acquisition of more and/or richer signals. Second, and perhaps more importantly, an extended juvenile period is also associated with more (allo)parenting and more explicit teaching behaviours, which directly facilitate language learning. In fact, teaching is often seen as one of the foundations of cultural transmission and knowledge sharing (Gweon, 2021; Hewlett & Cavalli-Sforza, 1986). In the case of language evolution via HSD, the rise of direct scaffolding of communication by parents and caregivers (e.g. child-directed speech) has been argued to provide children with the possibility to master increasingly semantically complex signals (Benítez-Burraco & Kempe, 2018). In other words, longer periods of learning together with child-directed speech facilitate the acquisition of increasingly rich languages, and in fact ensure their successful cultural transmission over generations.

Finally, domestication is typically associated with *enhanced playfulness* and the persistence of play behaviours across the lifespan, which can also impact learning and communicative inference (see Langley et al., 2019). The role of play and exploration in learning has been studied extensively in the context of education and child development, with play behaviours shown to support cognitive development by helping children reduce uncertainty, regulate emotions, boost their sensitivity to social signals, practice theory of mind and reasoning about other individuals' mental states, and improving their linguistic skills (Lewis et al., 2000; Lillard, 2017; Pelz & Kidd, 2020; Weisberg, 2015). With respect to language learning in particular, play behaviours can support language acquisition by increasing exposure to linguistic input and promoting the exploration of new constructions and new uses of known constructions. Besides facilitating the learning of more semantically complex languages by children, playful behaviours that persist through adolescence and adulthood can facilitate linguistic innovations that are then transmitted horizontally between peers and/or vertically across generations, shaping the structural characteristics of languages through a process of language emergence and change. Moreover, such enhanced playfulness in adulthood was also suggested to counteract tendencies towards dominance and to promote egalitarian and cooperative ways of living in hunter-gatherer communities (Gray, 2009).

In sum, we have highlighted four prominent features associated with self-domestication that can facilitate the social learning of increasingly semantically complex signals and promote communicative inference. These are reduced reactive aggression and increased prosociality (which clearly underlies most other features), buffered environment, extended juvenile period, and enhanced playfulness. Together, these

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features impact the process of communication and learning, and thus shape the cultural evolution of languages.

Open Questions and Future Directions

In this section, we highlight two open questions regarding the hypothesis that self-domestication is responsible for the evolution of human languages, and speculate on their potential implications for understanding the cultural evolution of language in our species.

The 'Self' in Self-domestication

The first problem is teasing apart the specific role and/or unique contribution of the notion of *self* in the *self*-domestication hypothesis. What exactly is the difference between animals that were involuntarily and intentionally domesticated by humans (e.g. dogs, birds) and self-domesticated animals (e.g. humans, and potentially also bonobos; see Hare, 2017; Hare et al., 2012; Kovalaskas et al., 2021), whose domestication process was triggered organically as a result of internal and unguided pressures? How do their environments differ, and how do these differences relate to the affordances and motivation for enhanced communication? Currently, these questions remain unanswered. No work to date has examined the potential implications of being a self-domesticated species *as opposed to* a domesticated one, and there has been no cross-species comparison of behavioural and genetic traits in domesticated versus self-domesticated species. In fact, the definition of being self-domesticated is simply exhibiting the typical features commonly associated with domestication in other animals (i.e. 'the domestication syndrome'), but without the obvious presence of a domesticator. While the end result of self-domestication and domestication processes seems to be similar, we know very little about the causes, environments, evolutionary trajectories, and physiological mechanisms that might differentiate them and trigger a process of self-domestication in a species.

With respect to the cultural evolution of language, this potential difference between domestication and self-domestication might be extremely important, and could shed light on why humans (but not other domesticated animals) possess such sophisticated linguistic abilities and open-ended productive languages. For instance, a self-domesticated species with increased prosocial tendencies and internal selection against aggression might be intrinsically more motivated to produce and refine highly informative yet compressible languages over time, as these would in turn facilitate more communication and cooperation between increasingly complex networks of individuals (see Figure 2). In other words, the need to develop richer languages is somewhat inherent to the process of self-triggered, enhanced sociality between members of the same species (and, consequently, to the process of self-domestication in that species). In sharp contrast, domesticated animals were artificially selected for tameness and for increased prosociality with respect to their relationship to humans, but not each other: serving either as human companions (e.g. dogs, cats), a food source for humans (e.g. sheep, goats, cows), or working aid for humans (e.g. horses, donkeys). As such, language evolution and cultural evolution might be unmotivated in these species.

While speculative, these unexplored potential differences might be the missing link for understanding the uniqueness of human languages. Notably, while other animals are also able to encode information using discrete (and sometimes even compositional) signals (Arnold & Zuberbühler, 2006, 2008; Suzuki, 2016), their communication systems are still remarkably different from humans' impressive repertoire of productive and rich signals. As a first step in understanding this gap, we suggest carefully examining other allegedly self-domesticated species (i.e. bonobos) and characterizing the ways in which their communicative systems and cultural evolution differ from their close relatives who have not undergone self-domestication (i.e. chimpanzees) (see also Whiten, 2019). While there are initial efforts to carry out

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such a cross-species comparison (Clay & Zuberbühler, 2020; Hare et al., 2012), much more research is needed in order to shed light on the evolution of humans' unique linguistic abilities, and in order to capture the potential contribution of self-domestication markers such as those we have highlighted above (e.g. buffered environment, extended juvenile period, enhanced play) to the process of language emergence via cultural evolution.

Self-domestication or Just Prosociality?

The second problem we want to highlight is the difficulty in identifying whether it is the domestication syndrome per se that is responsible for creating the needed conditions for language to evolve, or whether high prosociality is already enough for explaining the patterns we see in humans. In other words, is it even necessary to invoke the self-domestication hypothesis as a whole, or can enhanced social behaviour alone be enough to bring about the prerequisites needed for the cultural evolution of language? Here we draw on examples from other highly social species that also exhibit rich communication systems (e.g. dolphins, whales, elephants), but we suggest that a conclusive answer cannot be given since it is currently unclear whether these species are also self-domesticated or not.

For example, elephants live in complex social groups where adult females cooperate in group defence, offspring care, and resource acquisition, and were shown to possess a rich multimodal communication system that includes vocal, visual, tactile, and chemical signals that can encompass specific meanings and intents shared with other members of the herd (Kahl & Armstrong, 2000; Langbauer, 2000; Poole & Granli, 2011; Soltis et al., 2005a, 2005b; Stoeger, 2021; Wierucka et al., 2021). This complex signal system mediates the intricate teamwork displayed by members of an elephant family, including day-to-day decision-making such as deciding when and where to go or how to respond to predators (Jacobson & Plotnik, 2020). Moreover, elephants' communication systems show a great deal of variation across individuals and across different herds, which is seen as an important feature of human language (Evans & Levinson, 2009). Similarly, dolphins are generally more prosocial (Lalot et al., 2021) and have complex socially oriented communication systems (e.g. Papale et al., 2020), and whale songs are culturally transmitted and exhibit the kind of variability and rich structure we see in birdsong, suggesting a prominent role for social learning and culture in their development (Whitehead & Rendell, 2015; Garland et al., 2017).

If other highly social species display the critical features associated with human language and cultural evolution (such as social learning, cooperation, etc.), then perhaps enhanced prosociality is already enough to give rise to the inference skills and communication patterns that presumably enabled language emergence in our species. In line with this idea, some work has cast some doubt on whether self-domestication is needed for explaining general features of human social evolution, as these appear to be more similar to other social mammals than to other domesticated mammals (Shilton et al., 2020).

Notably, it is currently unknown to what extent human languages and their cultural evolution resembles other social animals' communicative systems. For instance, there has been little empirical work on the exact nature of elephant vocalizations beyond anecdotal evidence and subjective inference, and even less comparative work on the way these vocalizations may parallel human languages. More importantly, it is currently unknown whether highly social animals such as elephants and whales have also undergone a similar evolutionary process to self-domestication. It is in fact possible that selection towards reduced aggression always entails the emergence of features typically associated with self-domestication.

Supporting this idea, Raviv et al. (in press under preparation) used extensive cross-species and genetic comparisons to show that elephants do in fact exhibit many of the cognitive, behavioural, and physiological features associated with self-domestication, and that genes previously associated with domestication have been positively selected for and enriched in elephants. This work suggests that other highly social animals might have also been self-domesticated, and display the 'full package' of domestication as discussed above.

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Future research should test for self-domestication markers in other candidate species such as whales, and try to distinguish between different evolutionary paths towards increased prosociality.

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