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Survival of the Friendliest: *Homo sapiens* Evolved via Selection for Prosociality

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Annu. Rev. Psychol. 2017. 68:155–86

First published online as a Review in Advance on October 12, 2016

The *Annual Review of Psychology* is online at psych.annualreviews.org

This article's doi: 10.1146/annurev-psych-010416-044201

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Keywords

cognitive evolution, domestication, human evolution, self-domestication, social cognition

Abstract

The challenge of studying human cognitive evolution is identifying unique features of our intelligence while explaining the processes by which they arose. Comparisons with nonhuman apes point to our early-emerging cooperative-communicative abilities as crucial to the evolution of all forms of human cultural cognition, including language. The human self-domestication hypothesis proposes that these early-emerging social skills evolved when natural selection favored increased in-group prosociality over aggression in late human evolution. As a by-product of this selection, humans are predicted to show traits of the domestication syndrome observed in other domestic animals. In reviewing comparative, developmental, neurobiological, and paleoanthropological research, compelling evidence emerges for the predicted relationship between unique human mentalizing abilities, tolerance, and the domestication syndrome in humans. This synthesis includes a review of the first a priori test of the self-domestication hypothesis as well as predictions for future tests.

Contents

INTRODUCTION 156
PAN VERSUS *HOMO* SOCIAL UNDERSTANDING 157
Apes Take Others' Perspectives and Cooperate Flexibly 157
Only Human Apes Cooperatively Communicate 160
THE DOMESTICATION OF DOG SOCIAL COGNITION 160
Dogs Are Wolves Prepared to Cooperatively Communicate 161
Foxes Selected for Friendliness Cooperatively Communicate 161
Dog Self-Domestication 162
BONOBO SELF-DOMESTICATION 162
Sexual Selection of Friendlier Male Apes 162
A Priori Tests of Bonobo Self-Domestication 163
THE INFLUENCE OF HUMAN TEMPERAMENT ON MENTALIZING 164
THE HUMAN SELF-DOMESTICATION HYPOTHESIS 165
The First A Priori Test of Human Self-Domestication 167
The Eye of Cooperative Communication 168
Like-Me Psychology Drove Paleolithic Self-Domestication 170
Self-Control: The Unique Feature of Human Self-Domestication 172
Self-Domestication Through Evolutionary Development 173
CONCLUSION 175

"Man in many respects may be compared with those animals which have long been domesticated."

—Charles Darwin (1871)

INTRODUCTION

Darwin viewed the evolution of human intelligence and morality as the greatest challenge for his theory of evolution through natural selection (Darwin 1871). This remains the case today (MacLean et al. 2012). Our language and cultural cognition allows for cooperation and technology more complex than anything seen in nonhumans, yet our neurobiology, psychology, and genome are remarkably similar to other apes (Somel et al. 2013). A complete theory of human cognitive evolution needs to explain how these shared traits evolved into new forms of human cognition. To meet Darwin's challenge, we must identify derived cognitive features that evolved in our lineage and support our unique phenotype. Then we must identify the process by which these traits arose (Hare 2007, 2011). Adding to this challenge are discoveries suggesting that at least 10 different species evolved within the genus *Homo*. Modern theories of human cognitive evolution must now contend with growing evidence that *Homo sapiens* is just one among many human species that evolved. It is no longer enough to point out what makes us human. We must also determine what allowed our species to outlast as many as five other large-brained human species that shared the planet with us, some perhaps until as recently as 27 kya (Wood & Boyle 2016).

kya: thousands of years ago

This article reviews the latest research suggesting that early-emerging cooperative-communicative skills are responsible for unique features of human cognition and that our psychology evolved in large part due to selection for prosociality (i.e., positive but potentially selfishly motivated acts as opposed to antisocial interactions; Eisenberg et al. 1983). Comparisons of mentalizing skills between apes reveal that among apes, only human infants develop cooperative-communicative skills that facilitate human forms of cultural cognition; however, domestic dogs

possess some social skills that resemble those seen in human infants. Research with experimentally domesticated foxes and bonobos shows how selection for prosociality can lead to increases in the cooperative-communicative flexibility observed in dogs and infants. This comparative developmental work provides the basis for the self-domestication hypothesis, which proposes that unique human psychology evolved as part of a larger domestication syndrome that converges with other domesticated animals.

HSD: human self-domestication hypothesis

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 prosociality over aggression. As a result, modern humans possess traits consistent with the syndrome associated with domestication in other animals (**Table 1**). The HSD suggests this selective pressure also led to enhanced cooperation in intergroup conflicts. The hypothesis proposes that the reduced emotional reactivity that results from self-domestication and increased self-control created a unique form of human tolerance allowing the expression of more flexible social skills only observed in modern humans. Expanded developmental windows like those seen in domesticated animals allow this unique form of human tolerance and social cognition to develop and left *H. sapiens* as the last human standing (**Figure 1**).

PAN VERSUS *HOMO* SOCIAL UNDERSTANDING

Our ability to mentalize, or attribute mental states to others, is the foundation of cultural cognition (Herrmann et al. 2007). Humans develop the ability to recognize what others perceive, feel, intend, and know. Children begin in infancy to recognize that others can have mental states and even false beliefs that can differ from their own or reality. As adults, we rely on our ability to infer others' unobservable thoughts based on observable social cues and context. Our ability to reason about the minds of others allows for everything from imitation to deception, group coordination, teaching, and language acquisition (Seyfarth & Cheney 2014, Tomasello 2009b). Given the central role of these skills in human social cognition, tremendous energy has been focused on testing whether they are shared with other animals or are a derived feature of human cognition (Hare 2011).

Apes Take Others' Perspectives and Cooperate Flexibly

Beginning in the 1970s, chimpanzees (*Pan troglodytes*) quickly became central to studies of mental attribution because they provided a powerful phylogenetic test. The skills we share with chimpanzees were probably present in our last common ancestor, but the skills found only in humans help explain our explosive evolutionary success.

Initial research on chimpanzee theory of mind was as methodologically flawed as it was pioneering. It was only after researchers began taking an ecological approach to cognition that major advances were made in our understanding of chimpanzee mentalizing (Hare 2001, Whiten 2013). Chimpanzees failed to solve visual perspective-taking problems by cooperating and communicating with humans. However, they solved similar problems when placed in competition against each other. A series of competitive experiments show that chimpanzees are skilled at taking the perspective of others based on their current and previous perceptual experience (Hare 2011).

This led to more powerful methods using larger samples that also showed these skills in noncompetitive contexts (MacLean & Hare 2012). These spontaneous measures of social cognition ruled out the potential for simple behavior reading or learning within the experiment (Hare 2011; although see Povinelli & Vonk 2004).

Several studies have suggested that chimpanzees understand what others know, but there remains no compelling evidence for explicit false belief understanding in any animal, including great

Table 1 Evidence for domestication syndrome in modern humans

	Dog versus wolf[a]	Experimental fox versus control fox[a]	Bonobo versus chimpanzee[a]	Holocene humans versus Lower Paleolithic humans
Aggression	Lower-intensity inter- and intragroup aggression in feral dogs	Experimental but not control foxes are nonaggressive toward humans	Lower intensity inter- and intragroup aggression in bonobos	Intragroup tolerance allows and is favored due to demographic pressure in Holocene humans (Cieri et al. 2014, Henrich 2015)
Physiology	Dogs show a muted stress response when interacting with humans	Higher basal serotonin and lower corticosteroids in experimental foxes	Bonobos have more a passive coping response to social stress	Holocene humans exhibit morphologically inferred reductions in neonatal androgens and pubertal testosterone levels and increased brain serotonin and oxytocin availability (Cieri et al. 2014, Nelson et al. 2011)
Morphology	Dogs show reduced cranial capacity and depigmentation of the coat	Experimental foxes show a feminized skull and depigmentation of the coat	Bonobos show reduced cranial capacity, feminized faces, and depigmentation of lips and tail tufts	Holocene humans exhibit a modest reduction in cranial capacity, feminized faces, globular cranial development, and depigmentation of the sclera (Cieri et al. 2014, Hublin et al. 2015, Tomasello et al. 2007)
Prosocial behavior	Dogs are more attracted to humans than to conspecifics	Experimental foxes are more attracted to and interested in playing and interacting with humans as adults	Bonobos exhibit more play and sociosexual behavior as adults, voluntarily share food, and are more food tolerant	Holocene humans exhibit extreme levels of intragroup food sharing, helping, and social bonding (Kramer 2014, Warneken 2015)
Expanded developmental window	Period of socialization with humans begins earlier and lasts longer in dogs; dogs retain the juvenile vocal repertoire into adulthood	Period of socialization with humans begins earlier and lasts longer in experimental foxes; experimental foxes retain the juvenile vocal repertoire into adulthood	Nonreproductive sociosexual behaviors that create tolerance emerge early and last throughout adulthood in bonobos; cognitive skills related to spatial memory and social inhibition exhibit delayed development in bonobos	Holocene humans exhibit early-emerging social cognition and graded brain development with extreme delays in synaptic pruning of cortical regions (Casey & Caudle 2013, Somel et al. 2009, Wobber et al. 2014)
Social cognition	Dogs are more sensitive to human social cues	Experimental foxes are more sensitive to human social cues	Bonobos attend to eyes and exploit a human's gaze more and show increased cooperative flexibility	Holocene humans exhibit increases in cooperative communication, cultural ratcheting, and coordinated defense against out-groups, as well as expanded social networks (Cieri et al. 2014, Hare 2011)

[a]Nonhuman comparisons are based on Hare et al. (2012)

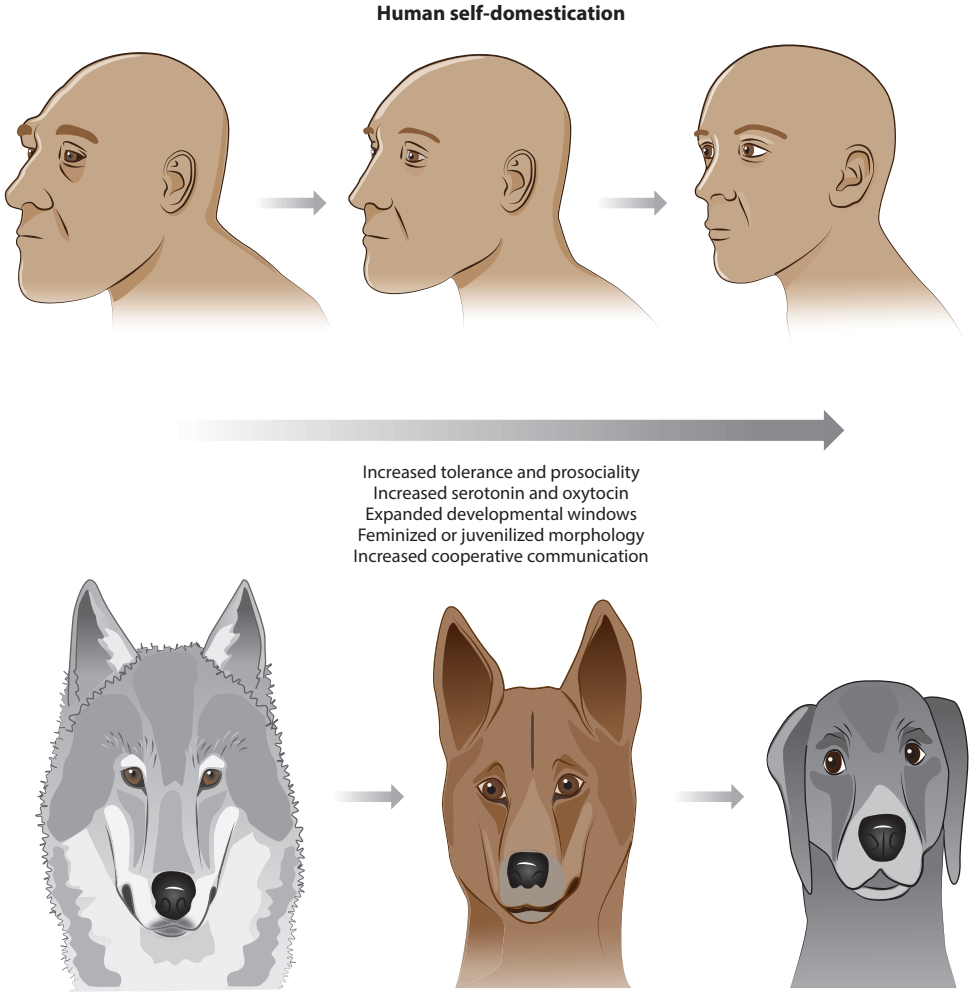


Figure 1

Homo sapiens evolved, in part, as a result of selection for increased in-group prosociality during the Paleolithic, leading to a variety of morphological, physiological, and cognitive changes also observed in domestic animals such as *Canis familiaris*.

apes (Hare 2011, Martin & Santos 2016). Further studies have shown that, in many contexts, chimpanzees behave similarly to human children when they attribute intentions to others. For example, chimpanzees are more patient with an experimenter who is unable to share food than with one who is clearly unwilling (Call et al. 2004).

These social cognitive skills are also applied flexibly to a number of cooperative situations. Chimpanzees can solve novel instrumental problems that require cooperation and helping (Hare & Tan 2012, Melis et al. 2010). They know when they need to recruit help, which potential helper is most skilled, and what leverage they have to negotiate between equal and unequal payoffs (Melis et al. 2006a, 2008, 2009). Chimpanzees are also capable of taking different roles in collaborative tasks (Melis & Tomasello 2013).

Taken together, chimpanzees are flexible in assessing what others perceive and intend. Although chimpanzees are skilled cooperators and take other's perspectives in noncompetitive contexts, it was initially easier to demonstrate many of their theory of mind skills in competitive tasks (Hare 2011).

Only Human Apes Cooperatively Communicate

Despite the social flexibility of chimpanzees, there are meaningful gaps in their understanding of and tolerance for others. Several studies show that, although chimpanzees can cooperate or communicate, they struggle to do both (Bullinger et al. 2014, Herrmann & Tomasello 2006, Melis et al. 2009). Central to this phenomenon is their inability to spontaneously and flexibly use gestures to find hidden food (Hare 2011). Human infants begin using other's gestures and producing them in their first year of life. Infants become part of the cultural world of adults by developing an understanding of the intention behind novel and arbitrary gestures. In contrast, while nonhuman apes can slowly learn to use cooperative-communicative gestures, it is extremely difficult for them to generalize what they learn to a new or arbitrary gestural signal (Call et al. 1998, Hare & Tomasello 2005b, Herrmann et al. 2007, MacLean & Hare 2015a; although see De Waal et al. 2008). This limitation is made worse by the inability of chimpanzees to remain tolerant during cooperative activities. Although chimpanzees are skilled at using other chimpanzees as social tools, cooperation breaks down when the reward for joint effort becomes easily monopolized (MacLean & Hare 2013). Chimpanzees are constrained in their ability to inhibit intolerance toward potential cooperative partners even when they know they cannot solve a problem alone. Only a small minority of chimpanzee dyads within a group are tolerant enough to work for sharable food and no dyad can cooperate once rewards require active sharing or turn taking (Hare et al. 2007, Melis et al. 2006b). This intolerance and inflexibility in cooperative-communicative contexts likely prevent chimpanzees from sharing intentions and building on previous innovations in a process known as cultural ratcheting (Hare 2011).

THE DOMESTICATION OF DOG SOCIAL COGNITION

Domestic dogs are more skillful at using human gestures than nonhuman apes (Hare et al. 2002). Dogs follow the direction of a human gaze or point to locate hidden food or toys. If a human points to one of two locations, dogs are more likely to search where a human has indicated. Dogs can even spontaneously use novel and arbitrary gestures to help direct their search for objects or food. Several controls rule out the possibility that these searches in response to human gestures are reflexive or based on olfactory cues (Hare & Tomasello 2005b). Another similarity between dogs and infants is that both commit the A not B search error when directed by a human in the classic Piagetian task. Like human children in this task, dogs search in a hiding location that has repeatedly been baited in the past over a new location they observe being baited (Topál et al. 2009). Dogs are also the only nonhumans capable of fast mapping. In a way similar to the way young children learn words, several border collies have acquired hundreds of object labels using the principle of exclusion after single interactions with each new toy (Kaminski et al. 2004). Dogs seem to understand the cooperative-communicative intent of human signals in ways resembling those of the youngest human infants. This raises the question of how such a distantly related species can show skills that are crucial to human social cognitive development (Kaminski & Marshall-Pescini 2014). Comparisons of canids have revealed an important process by which social cognition evolves.

Dogs Are Wolves Prepared to Cooperatively Communicate

Dogs do not need intensive exposure to humans to begin using our gestures. Dog puppies also show skill at using basic human gestures (Hare et al. 2002). Although variance exists among individual dogs, as a species, dogs rely on human gestures even as puppies (Hare et al. 2010, Stewart et al. 2015, Wobber et al. 2009). Dogs did not inherit this early-emerging pattern from wolves. The skills of wolves at reading human gestures are more similar to those of nonhuman apes than to those of dogs. To develop skills in reading human gestures, wolves require intensive human socialization during a short critical period; as the window of socialization closes, they show little skill at understanding humans without explicit training as adults (Gacsi et al. 2005, Hare et al. 2002, Viranyi et al. 2008). Unlike dogs and infants, wolves do not commit the socially mediated A not B error (Topál et al. 2009). The independence of wolves from humans also means that when faced with an impossible task, they continue to try to solve the problem without help, whereas dogs quickly look to a human for help (Miklósi et al. 2003).

Foxes Selected for Friendliness Cooperatively Communicate

Because the early-emerging skill at reading gestures is not observed in wolves, the unusual social skills of dogs probably appeared during domestication (Hare et al. 2010). This hypothesis was tested by examining the cooperative-communicative abilities of an experimental line of foxes that had been intensively selected to be attracted to and nonaggressive toward people for 45 generations (Trut 1999). The experimental line was compared to a control line bred randomly for how they respond to humans. As a result of this selection, the experimental line is highly prosocial toward humans and exhibits a suite of phenotypic traits known as the domestication syndrome (**Table 1**). In comparison to the control line, the experimental foxes show the expected increases in approach toward humans. However, they also show a high frequency of traits not intentionally selected, including physiological, morphological, developmental, and behavioral changes also seen in domestic animals. This domestication syndrome includes increased brain serotonin levels and reductions in hypothalamic-pituitary-adrenal axis reactivity. Morphologically, the experimental foxes show increased frequencies of piebald coats, star mutations (white spots on the forehead), shorter muzzles, feminized faces, floppy ears, and curly or shortened tails (Trut et al. 2009). Developmentally, most traits in the experimental foxes appear to relate to expanded developmental windows. Experimenters can socialize experimental foxes earlier in development and the period of socialization remains open for much longer (i.e., similar to that of dogs) (Belyaev et al. 1985). Adult experimental foxes use juvenilized vocalizations and social behaviors such as tail wagging far more frequently when approached by humans than adult control foxes do (Gogoleva et al. 2008). When tested on the same cognitive measures of cooperative-communication used with apes, dogs, and wolves, fox kits from the experimental line are more skilled than same-age control kits. The experimental foxes spontaneously use basic human gestures in two different paradigms and perform similarly to dog puppies of the same age. Controls demonstrate that the experimental and control foxes are similarly motivated even though only the experimental line responded to human gestures. Although the experimental line was never selected (or even evaluated) on the basis of their cooperative-communicative abilities with humans, experimental kits perform like dog puppies when responding to human gestures (Hare et al. 2005).

The foxes' performance with human gestures supports the hypothesis that dogs' social skills evolved not only during domestication but also as a result of it. The fox experiment demonstrates that selection on emotional reactivity changes not only temperament but also a suite of unrelated phenotypic traits as a correlated by-product of this selection. The more flexible skills of cooperating and communicating with humans probably represent another of the by-products of this selection

for friendliness. Foxes, like most mammals, use the social cues of conspecifics, but due to selection for prosocial interactions with humans, these old cognitive skills are applied in a new interaction with a new social partner (Hare & Tomasello 2005a).

Less reactive temperament likely replaced fear with an attraction to humans as selection acted on developmental pathways. Shifts in development, especially early in fetal development, can alter emotional reactivity and are thought to create a cascade of unselected consequences throughout the phenotype (Price & Langen 1992, West-Eberhard 2003, Wilkins et al. 2014). For example, the neural crest hypothesis suggests that the domestication syndrome is a result of changes in the migration pattern of melanocytes during neural crest formation, which simultaneously affects neurohormone levels, pigmentation, and morphology early in development (Wilkins et al. 2014), although not in a universal pattern across domestic mammals (Sanchez-Villagra et al. 2016).

Dog Self-Domestication

Based on the fox findings, it might be that dog cognition also evolved as a by-product of selection on emotional reactivity. However, in the case of dog evolution, natural selection acted on the temperament of wolves. Wolves with a temperament allowing them to approach human settlements showed higher reproductive success and favored self-domestication (as do species adapting to urban environments today; Ditchkoff et al. 2006). A population of wolves able to exploit the new niche of scavenging food remains and feces became more tolerant of humans and could be discriminated from other wolves due to morphological traits associated with the domestication syndrome. This new interaction with humans allowed old cognitive abilities to be expressed in a new context and resulted in more flexible social problem solving with humans. As the constraint of temperament was lifted, heritable variance in these newly revealed social skills may have been targeted by selection (Wobber et al. 2009). Thus began the most successful interspecific cooperative-communicative relationship in mammalian evolutionary history (Hare et al. 2010, Hare & Woods 2013; although see Udell et al. 2010). This led to a bond so strong that exogenous administration of oxytocin in dogs also modulates increases in mutual gaze, physical contact, and endogenous oxytocin expression in the humans with which they interact (Nagasawa et al. 2015). Not only have the emotional systems of dogs evolved but they have also hijacked our emotional systems for at least 15,000 years (MacLean & Hare 2015b).

BONOBO SELF-DOMESTICATION

The experimental foxes and dog self-domestication both imply that natural selection can lead to increases in prosocial over aggressive behavior, which can in turn lead to domestication syndrome (**Table 1**). The self-domestication hypothesis predicts that natural selection would also have shaped other species for increases in prosociality. Bonobos (*Pan paniscus*), one of our two closest living relatives, have been identified as a likely candidate for self-domestication (Wrangham & Pilbeam 2002).

Sexual Selection of Friendlier Male Apes

Bonobos differ from chimpanzees in their aggressive behavior (Hare et al. 2012). No bonobo has ever been observed to kill another bonobo (although for a potential exception see Wilson et al. 2014). Unlike chimpanzees, male bonobos do not coerce females, commit infanticide, or target their own mothers for aggression. Also unlike chimpanzees, male bonobos do not form coalitions with one another within their groups but instead rely on their mother's status to gain access to

females (Surbeck et al. 2011). Finally, unlike chimpanzees, male bonobos do not participate in border patrols or lethal raids into neighboring territories.

Hare et al. (2012) proposed that male bonobos evolved to be more prosocial through sexual selection. Living in a richer and more predictable ecology, unrelated female bonobos formed bonds that allowed them to respond to male aggression in a way that female chimpanzees cannot. Although wild female chimpanzees rarely support other females when they are targeted by aggressive males, similar coercion by male bonobos is met by female coalitionary defense (Tokuyama & Furuichi 2016). Similarly, female bonobos do not tolerate male aggression toward juveniles and infants (Hare & Yamamoto 2015, Walker & Hare 2016). According to the self-domestication hypothesis, bonobos evolved to be less aggressive because females were able to express a preference for less aggressive males.

A Priori Tests of Bonobo Self-Domestication

After Wrangham & Pilbeam (2002) initially proposed that bonobos could be a candidate for self-domestication, a number of a priori tests examined whether derived features of the bonobo phenotype fit the expected pattern of domestication syndrome (**Table 1**).

Hare et al. (2012) reviewed the evidence that differences between bonobo and chimpanzee prosocial behavior, physiology, morphology, development, and cognition support self-domestication. Bonobos are more tolerant than chimpanzees when sharing food because bonobos use sex and play to reduce social tension when conflicts arise (Hare et al. 2007; although see Jaeggi et al. 2010). Bonobos also voluntarily share food. When given the choice of either eating preferred food before their morning meal or opening a one-way door to allow another bonobo to share the food, bonobos prefer to eat together. When bonobos can choose to open a door for either a group member or a stranger, they prefer to share with another bonobo with which they have never physically interacted (Tan & Hare 2013). This level of xenophilia contrasts with the xenophobia that chimpanzees show toward strangers (Wilson et al. 2014).

The unusual sharing observed in bonobos is modulated by their physiological response to social stress. Before a dyad of male bonobos is released into a room with food, they show increases in cortisol, associated with a stress response, but not testosterone, typically associated with agonism. The increase of cortisol in male bonobos promotes tolerance by creating a passive coping style that encourages social contact to reduce anxiety through sociosexual behavior (likely by releasing the anxiolytic oxytocin). Chimpanzee males show the exact opposite response. The testosterone reactivity seen in chimpanzee males reduces the potential for tolerance because it primes them for competition as they strive for higher status (Van Honk et al. 2010, Wobber et al. 2010a).

Neurobiologically, bonobos resemble animals that show increased serotonin levels and concomitant reductions in anxiety and aggression as the first sign of domestication (i.e., Agnvall et al. 2015, Plyusnina et al. 1991). Although levels of serotonin in the cerebrospinal fluid have not been directly measured due to the obvious ethical concerns, postmortem neuroanatomical studies have found that bonobos have twice the density, relative to chimpanzees, of serotonergic axons in the basal and central nuclei of the amygdala (Rilling et al. 2011, Stimpson et al. 2015). This is a pattern consistent with a species where social frustration is less likely to lead to aggression (Bernhardt 1997).

Morphologically, bonobos show features associated with self-domestication, including reduced cranial size, canine dimorphism, and depigmentation of the lips and tail tufts. Bonobos also show evidence of an expanded window of social development for behaviors involved in generating tolerance. Bonobos exhibit early-emerging sociosexual behaviors that are used in infancy to mitigate the risk of social conflict while sharing food. They also retain nonreproductive sociosexual and

play behaviors into adulthood that act to maintain tolerance. In contrast, chimpanzees show no sociosexual behavior in infancy, only demonstrating this behavior during reproductive bouts as adults (Wobber & Hare 2015, Woods & Hare 2011).

Cognitively, bonobos illustrate the connections between temperament, tolerance, and social cognition. Temperamentally, bonobos are more cautious and observant toward novelty than other apes, with the exception of human children (Herrmann et al. 2011). Although bonobos do not differ from chimpanzees in their use of human cooperative-communicative gestures, they are more sensitive to human gaze direction (MacLean & Hare 2015a). Bonobos are more likely to co-orient in response to a shift in a human's gaze direction or to respond appropriately to their intentions in action (Herrmann et al. 2010). Eye tracking comparisons between bonobos and chimpanzees show that bonobos focus more on the eyes of people whereas chimpanzees tend to focus on the mouths of the same people (Kano et al. 2015). Bonobos also show more flexibility than chimpanzees in instrumental cooperative tasks that require feeding tolerance. Whereas even the most experienced chimpanzee cooperators fail to cooperate to obtain monopolizable food, experimentally naïve bonobos succeed. Even when small amounts of prized food (four apple pieces) are placed in one easily monopolizable location, bonobos cooperate and, on average, split the reward in half. The temperament of bonobos, which is conflict averse and uses social interaction to ease tension, allows them to solve more cooperative problems with a wider range of social partners than chimpanzees (Hare et al. 2007).

Bonobos also show developmental delay across a number of cognitive domains related to foraging and feeding competition—they are particularly uninhibited in social contexts as a result (Rosati & Hare 2012, Wobber et al. 2010b). This lack of inhibition likely presents a major constraint on the cooperative-communicative abilities of bonobos relative to humans. Hare et al. (2012) interpret these and other a priori tests as overwhelming support for bonobo self-domestication. This raises the possibility that other apes may have been affected by the same process during selection for increased prosociality.

THE INFLUENCE OF HUMAN TEMPERAMENT ON MENTALIZING

Studies of nonhuman apes suggest that cooperative-communicative forms of mentalizing evolved in our genus and are important to our cognitive sophistication. These studies also show that tolerance is a constraint on cooperation and communication in nonhumans. In bonobos, dogs, and foxes, natural or artificial selection for prosociality has led to increases in tolerance and social cognitive flexibility in association with the domestication syndrome.

On the basis of this type of comparative work, Hare & Tomasello (2005a,b) proposed the emotional reactivity hypothesis. This hypothesis suggests that human levels of cooperative communication were a result of an increase in social tolerance generated by a decrease in emotional reactivity. Without tolerance, advanced computational or social cognitive abilities would not be of much use because individuals could not share the benefits of joint effort. According to this hypothesis, an increase in tolerance in humans allowed inherited cognitive skills to be expressed in new social situations. Selection could then act directly on revealed variance in these newly expressed cognitive abilities.

Taking advantage of individual differences in human responses to novel or startling situations (Kagan & Snidman 2009), Wellman and colleagues conducted an a priori test of the predicted relationship between emotional reactivity and theory of mind development in human infants (Wellman et al. 2011). Children were observed for their interactions with others and then tested on false belief tasks. Consistent with the hypothesis, infants with the least aggressive and most socially reserved temperaments show the earliest expression of the false belief understanding that supports cooperative forms of communication—including language (Lane et al. 2013, Mink

et al. 2014, Wellman et al. 2011). Related findings come from an fMRI study of adults. After being provoked in a competition game, women who were highly reactive in a startle test showed the least activity in the temporal parietal junction (TPJ), medial prefrontal cortex (mPFC), and precuneus (PC) when deciding how to punish other women. These highly reactive women had the least activity in the cortical hubs of the brain's mentalizing network. In contrast, even after being provoked, women with low reactivity had high activity in their mentalizing network. Low reactivity led to more tolerance of provocation and more mentalizing (Beyer et al. 2014).

TPJ: temporal parietal junction

mPFC: medial prefrontal cortex

PC: precuneus

Individual differences in this temperament–social cognition axis supports the idea that changes in human social cognition relied on shifts in the hormonal and subcortical profiles (e.g., amygdala reactivity) linked to temperament. Evolutionary shifts in hormonal or neuropeptide expression or receptivity are evolutionarily labile and, as demonstrated in domesticated animals, can dramatically alter prosociality and are believed to produce a cascade of correlated phenotypic effects.

Because human and nonhuman social behavior are modulated by neurohormones, a number of hormones and neuropeptides are potential targets for prosocial selection. Serotonin, testosterone, and oxytocin are among the most important interactants mediating aggressive behavior (Kuepper et al. 2010, Montoya et al. 2012). In experimental animal populations selected for friendliness toward humans, increases in brain levels of serotonin are the first physiological sign of reduced emotional reactivity and aggression (Agnvall et al. 2015, Plyusnina et al. 1991). Exogenous serotonin in people (i.e., citalopram) increases harm avoidance and cooperative behavior during moral dilemmas and cooperative economic games (Crockett et al. 2010, Wood et al. 2006). Low testosterone is related to male prosociality and parental care (Burnham 2007). Exogenously administered oxytocin in humans reduces aggression directed toward in-group members compared to individuals from out-groups (De Dreu & Kret 2016). Selection for increased prosociality could have readily acted on any of these hormones to increase tolerance through decreased emotional reactivity. The changes in developmental pathways needed to alter emotional reactivity can then have widespread effects throughout the phenotype, including effects on social cognition.

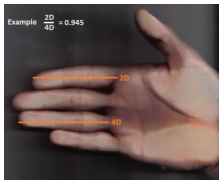
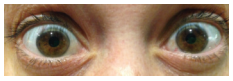
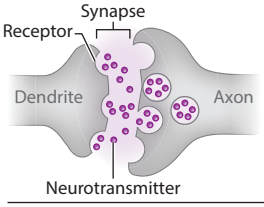
THE HUMAN SELF-DOMESTICATION HYPOTHESIS

The HSD builds on the work of Hare & Tomasello (2005b) and Hare et al. (2012) by proposing that modern humans were selected for prosociality. This hypothesis is inspired by the unusual level of intragroup tolerance and cooperation in modern humans and the link between temperament and social cognition demonstrated in animals and humans. The HSD predicts evidence for (*a*) selection for prosocial behavior linked to derived human cooperative-communicative abilities and (*b*) the domestication syndrome in our morphology, physiology, development, and cognition, as seen in other self-domesticated species (**Table 1**) (Wrangham 2014).

Evolutionary shifts in hormonal profiles related to tolerance and cooperation should be identifiable by using the morphological signatures of these changes found in the fossil record as well as by using genetic comparisons (see **Table 2**). The HSD goes beyond the emotional reactivity hypothesis proposed by Hare & Tomasello (2005b) in recognizing the likelihood that interaction between subcortical and cortical pathways led to unprecedented human tolerance. The HSD predicts that humans have reduced reactivity that increases the reward for social interactions, but it also predicts that, unlike any other domestic species, human tolerance is also due to massive increases in inhibition. The HSD suggests that it is this self-control combined with reduced reactivity that creates the human-specific adaptation for more flexible tolerance and unique forms of human social cognition.

The HSD may play a role in explaining three major moments in human cognitive evolution: (*a*) the initial appearance of the human adaptive package in *Homo erectus*, (*b*) increases in brain

Table 2 Morphological signals of increased tolerance and cooperative-communicative abilities in *Homo sapiens*

Image	Morphological trait	Changes indicated	Time of appearance	Reference
	Reduction in brow ridge and facial length	Reduced pubertal androgens and less despotic behavior in males	Middle/Upper Paleolithic	Cieri et al. 2014
	2nd digit to 4th digit length ratio (2D4D)	Reduced prenatal androgens and increased sensitivity to social cues	After the split from Neanderthals	Nelson et al. 2011
	White sclera	Increases in oxytocin and mutual gaze	Predicted: after the split from Neanderthals	Tomasello et al. 2007
	Globular cranial development	Early emergence of social cognition and the brain's social network	After the split from Neanderthals	Hublin et al. 2015
	Extended synaptic pruning	Late onset of adult self-control	Predicted: after the split from Neanderthals	Casey 2015
	Absolute brain size increase	Increase in self-control and social tolerance	Predicted: beginning with the appearance of genus *Homo*	MacLean et al. 2014

size between 2 million years ago and 80 kya, and (*c*) the lag between reaching the lower range of modern human brain size 500 kya and the expression of full-blown modern cultural behavior approximately 50 kya. Although all three moments are touched on in this review, the focus is largely on HSD as an explanation for the paradox of behavioral modernity in late human evolution (i.e., the temporal gap between the appearance of human morphology and the consistent expression of modern behavior). This is where the HSD currently provides the most testable predictions. In the following sections, I review an initial a priori test of the core predictions of the HSD and then examine morphological, physiological, and developmental evidence that can be interpreted

in favor of the HSD being an explanation of the appearance of modern human behavior in the Later Stone Age/Upper Paleolithic.

The First A Priori Test of Human Self-Domestication

Largely based on artifacts in the fossil record, researchers have inferred that behavioral modernity (i.e., the persistent establishment of behaviors requiring extremely flexible forms of causal reasoning, episodic memory, symbolic thought, etc.; McBrearty & Brooks 2000) and cultural diversity did not occur for several hundred thousand years after human brain size reached within the lower end of the current modern range (Holloway 2015; although see Schoenemann 2006). Cieri et al. (2014) explored the possibility that the explosion of cultural artifacts beginning around 80 kya occurred due to selection for temperament that allowed more cooperative communication and promoted rapid transmission of innovations.

Both theoretical models and ethnographic studies suggest that the modern toolkit was a product of demographic expansion (Henrich 2015). Before the Upper Paleolithic, *H. sapiens* transitioned from a low-density distribution to a larger, high-density distribution across a greater range of ecologies. This created a larger network of innovators and resulted in the technology revolution of the Upper Paleolithic.

The challenge for this hypothesis is explaining the sudden appearance of cultural ratcheting as competition for scarce resources increased with population density (Cieri et al. 2014). Without extreme levels of social tolerance, this type of competition would not only impede the social transmission of innovations but also prevent prosocial interactions (i.e., Aureli & De Waal 1997, Horner 2010). Cieri et al. (2014) predicted that an increase in tolerance and demographic pressure allowed a wider network of demonstrators to interact and learn from each other. This allowed existing cognitive skills to be expressed in a wider range of contexts across a broader social network.

Both testosterone and serotonin affect craniofacial morphology during development. Large pubertal spikes in testosterone are associated with an enlargement in the suborbital torus, or brow ridges, and elongated upper faces (Cieri et al. 2014). When facial features are manipulated in photos, people judge the exaggerated facial features produced by pubertal testosterone as being more aggressive and less trustworthy (e.g., Wilson & Rule 2015). Serotonin also plays a role in the early human fetal development of craniofacial morphology, although the mechanism is less well understood. Women taking selective serotonin reuptake inhibitors such as citalopram (an antidepressant medication) have an increased risk of giving birth to infants with reduced cranial size (Alwan et al. 2007). These craniofacial changes in humans echo those in domesticated animals and bonobos, in which an increase in serotonin and reduction in testosterone are associated with facial feminization and reduced cranial capacity (Hare et al. 2012).

Cieri et al. (2014) compared brow ridge size and facial width and length in fossil humans and modern humans. They predicted increasingly hypoandrogenized facial features across late human evolution. They also predicted reduced cranial capacity in Holocene humans, as observed in other domesticated animals.

In 13 modern human fossil crania from the Middle Stone Age and Middle Paleolithic (prior to 80 kya), 41 Later Stone Age/Upper Paleolithic (38–10 kya) crania, and more than 1,300 Holocene (less than 10 kya) crania, a temporal decrease in brow ridge size and the length of the face was observed. The brow ridge projection index of the Middle Stone Age sample was 1.5 standard deviations above that of the Late Stone Age sample and as much as 3.0 standard deviations above the Holocene samples. This difference was present in both the hunter-gatherer and agricultural subsamples within the recent human sample.

2D4D: relative length of the second digit (index finger) to the fourth digit (ring finger)

Facial length followed a similar pattern, with substantial facial shortening after 80 kya. The most extreme facial shortening was in modern hunter-gatherers. Agriculturalists seem to regress and develop slightly longer faces than hunter-gatherers. Replicating previous analysis, modern hunter-gatherers and agriculturalists both had smaller cranial capacity than the Late Stone Age humans (Leach 2003, Zollikofer & Ponce de Leon 2010).

It is also important to note that while Cieri et al. (2014) confined their analysis to modern humans, these results would have been far more extreme if they included similar comparisons to *Homo neanderthalensis* and *Homo heidelbergensis*. Although both archaic human species had similar-sized brains compared to *H. sapiens*, their faces are far more masculinized than the oldest modern humans (Churchill 2014).

Other biomarkers suggest reduced intrasexual competition and androgen exposure in modern humans. Compared to Neanderthals and other hominins, the 2D4D ratio, the relative length of the second digit to the fourth digit (i.e., the index and ring fingers), of modern humans suggests low prenatal androgen exposure in utero (McIntyre et al. 2009, Nelson et al. 2011). In mammalian testes, comparisons of gene expression profiles across development also suggest pedomorphism in human testis development. Human gene expression is more similar to adolescent mice than to chimpanzees that have gene expression profiles similar to other species with high levels of intrasexual competition (Saglican et al. 2014).

Fossil evidence suggests craniofacial feminization occurred just as cultural ratcheting was pushing us toward behavioral modernity. When human populations became increasingly connected and concentrated at high densities during the Holocene, human brains were reduced in size, which in other species is associated with an increase in serotonin. Although brain size generally increased during the evolution of *Homo*, there was a modest reduction in brain size late in human evolution that resembles reductions in domesticated animals. The 2D4D digit ratio and testis development support a shift in intrasexual competition and androgen exposure. The more masculinized 2D4D pattern in Neanderthals suggests this shift occurred late in human evolution.

The observed morphological changes in modern humans support the HSD. Selection likely modulated tolerance with increased serotonin levels and a reduction in androgen exposure. Males in particular must have been less aggressive in dominance interactions. The new level of tolerance resulted in old cognitive abilities being used more flexibly in new social contexts. Any heritable variance in these new skills, revealed when the constraint of intolerance was lifted, could then become the direct target of selection.

The Eye of Cooperative Communication

In the past two decades, another morphological signal of human cognitive evolution has been discovered. Of the dozens of primate species examined, only humans fail to produce eye-sclera pigment (Kobayashi & Kohshima 1997, 2001). All primates except humans pay a metabolic cost to hide the social information contained in the direction of their gaze by producing melanin (Kobayashi & Kohshima 2001). Humans have white sclera and an elongated eye shape that contrasts with the surrounding facial pigment and advertises the direction of our attention. Individual differences in levels of sclera melanin in nonhuman apes suggest heritable variability across hominoids (Mayhew & Gómez 2015).

Humans show an early-emerging and subconscious preference for eyes with white sclera that persists into adulthood. Infants show a preference for looking at white sclera in their first weeks (Farroni et al. 2004). Infants prefer to look at faces with white sclera and dark pupils over eyes with an inverted pattern of coloration (i.e., black sclera, white pupils) (Farroni et al. 2005). Children prefer stuffed animals with white rather than darkened sclera. Adults share this preference but are

unaware that their attraction is driven by the presence of white sclera (Segal et al. 2016, Whalen et al. 2004). By 7 months old, infants rely on white eye sclera to encode emotional cues using the same cortical network observed in adults (Grossmann et al. 2008, Jessen & Grossmann 2014).

Comparisons between human infants and nonhuman apes show that, although all species follow gaze direction, only humans prioritize eye direction over facial direction when coorienting to another's gaze. The increased reliance of infants over other apes on eye gaze is probably facilitated by our white sclera (Tomasello et al. 2007).

Our visible eyes provide information about eye direction and cues of mutual gaze that seem crucial to our unique forms of learning, cooperation, and communication (Grossmann 2016). Joint attention, which allows children to learn the association between labels and objects, relies on a child's ability to follow an adult's line of gaze (Tomasello 2009a, Tomasello & Farrar 1986). Mutual gaze is critical to the formation of shared intentions—a central psychological mechanism allowing for the development of unique human forms of cooperative communication (Tomasello et al. 2005).

White sclera may increase the potential for joint attention by enhancing eye-blink synchronization. When eye blinking is synchronized, humans improve the coordination of their subsequent motor activities. This synchronization is thought to lead to a Hebbian association (i.e., neural synchronization) between the activity in the inferior frontal gyrus of two people locked in mutual gaze. This interneural synchronization may prime other regions of the brain's social network and facilitate shared intentions between individuals (Koike et al. 2016). White sclera may serve to increase the likelihood and length of this synchronization.

Visible eyes also promote cooperative behavior in humans. People donate more in a public goods game when they are watched by a robot with large eyes. Subjects whose computer screens display a robot with oversized white sclera donate ~30% more to the public good than those without the robot on their screens (Burnham & Hare 2007). When a picture of human eyes was placed above a public bicycle rack or on a paper leaflet, bike theft was eliminated and littering reduced. In the controls without the eye manipulation, more bikes were stolen and there was more littering (Bateson et al. 2015, Nettle et al. 2012).

Eyes with white sclera favor expression of prosocial behavior. Visible human eyes facilitate cooperation by signaling the potential for social sanctions or reputational consequences. These signals probably affect human cooperation subconsciously (Burnham & Hare 2007; although see Fehr & Schneider 2010, Jessen & Grossmann 2014).

Depigmentation of human sclera may be a by-product of self-domestication because selection against aggression alters melanin expression. Furthermore, scleral tissue originates from the neural crest (Seko et al. 2008, Wilkins et al. 2014). If shifts in melanocyte migration of scleral tissue produced variance in white sclera as a result of self-domestication, selection could subsequently act directly on any heritable variance (West-Eberhard 2003).

Given the role of neuropeptides and hormones in mediating human gaze behavior, prosociality and white sclera likely coevolved. In particular, oxytocin is known to modulate mutual gaze and increase attention to the eyes of others in humans (Gamer et al. 2010, Guastella et al. 2008). In experiments in which human males examined only the eye region of people making different emotional expressions, exogenous administration of oxytocin improved the ability of the participants to infer the other person's affective state (Domes et al. 2013, Meyer-Lindenberg et al. 2011).

Effects of exogenous oxytocin seem specific to improving social memory of faces rather than to improving memory more generally (Rimmele et al. 2009). Oxytocin also facilitates bonding of parent and offspring through touch and mutual gaze (Baribeau & Anagnostou 2015, Carter 2014). This may explain increases in trust during cooperative games in subjects that have been given intranasal oxytocin (Kosfeld et al. 2005). The role of mutual gaze and oxytocin in the human–dog

bond demonstrates that this effect even extends to human–animal interactions (Nagasawa et al. 2015, Waller et al. 2013).

STS: superior temporal sulcus

The HSD predicts that increasing oxytocin levels, receptor densities, or receptor responsiveness in the brain was a crucial step in promoting the evolution of human prosociality (Baribeau & Anagnostou 2015). These increases would have promoted the use of eye gaze and favored the evolution of white sclera, allowing the close interactions that led to the social bonding and cooperative communication necessary for the expression of modern human behavior.

Like-Me Psychology Drove Paleolithic Self-Domestication

Humans are helpful or hurtful toward others based on perceived similarity to themselves. As adults, this like-me psychology manifests itself as in-group favoritism across a variety of contexts and cultures (Mullen et al. 1992). This favoritism results in a high degree of tolerance toward in-group members that facilitates unique forms of collaboration and conformity (Burton-Chellew & West 2012, Kurzban et al. 2015). In contrast, ostracism and lethal aggression among hunter-gatherers primarily targets nonconformist or out-group members (Boehm et al. 1993, Wrangham 1999). This type of antisocial or agonistic response is facilitated by the readiness of humans to dehumanize out-group members or those that dehumanize their own in-group (Hodson et al. 2014, Kteily et al. 2016).

This in-group versus out-group preference appears early in development, which suggests that humans are prepared for social discrimination based on like-me preferences (Bloom 2013, Mahajan & Wynn 2012). The latest neurobiological evidence and evolutionary models suggest that intragroup prosociality can explain our paradoxical kindness and cruelty toward others. Selection for in-group prosociality drove late human self-domestication and, as a correlated by-product, is responsible for extreme forms of out-group aggression.

Spontaneous sharing and helping develops early in infancy along with an in-group bias (Hamlin & Wynn 2011, Hamlin et al. 2007, Kinzler et al. 2011, Warneken 2015, Warneken et al. 2007). Nine-month-old infants prefer puppets that help another puppet who shares the child's food preference but also prefer puppets that harm another puppet with a dissimilar food preference (Hamlin et al. 2013). In sharing games, children as young as 5 years old prefer to share with in-group members, whereas 6-year-olds are more willing to pay a cost to punish selfish out-group members than in-group members (Engelmann et al. 2013, Jordan et al. 2014). Children also seem selective in enforcing norms depending on a violator's group affiliation (Schmidt et al. 2012). This early-emerging expression of in-group bias supports the idea that we are biologically prepared to support in-group cooperation and communication.

The neurobiology of this like-me psychology is also present in adults. A cortical network allows for the attribution of mental states and is built from regions specialized in social decision making (Adolphs 2009, Carter & Huettel 2013). Brain imaging using fMRI scans shows involvement of the mPFC, TPJ, and superior temporal sulcus (STS) in tasks requiring subjects to model the intentions, emotions, and beliefs of others (Amodio & Frith 2006, Harris & Fiske 2009). Ventral areas of the mPFC also show activity when people think about their own thoughts or emotions about others (Cikara et al. 2014b).

This cortical network allows people to compare their own thoughts and feelings to those of others and is central to generating both compassionate and dehumanizing responses. When other humans are perceived as having good intentions (being warm) and having the capability to carry them out (being competent), the mPFC is heavily involved in modulating empathic responses. In contrast, the mPFC becomes less active when people are shown photos of individuals perceived

as incompetent and cold (i.e., homeless people, drug addicts), and the amygdala and insula that encode disgust become the most active regions (Harris & Fiske 2006, Rilling et al. 2008a).

When subjects were allowed to punish in-group and out-group members for norm violations, punishment of in-group members was less likely and was associated with heightened activity and connectivity between the mPFC and TPJ. Mentalizing regions become more active, suggesting that people were justifying their groupmates' infractions; the same regions were not as active when out-group members made the same transgression (Baumgartner et al. 2012). When there is decreased activity in this mentalizing network, people are able to dehumanize others and are less likely to show empathy, tolerance, or prosociality (Baumgartner et al. 2012, Cikara et al. 2014a, Fiske et al. 2007, Harris & Fiske 2009, Waytz et al. 2012).

The neuropeptide oxytocin is the strongest candidate for explaining the human-unique pattern of empathy and dehumanization. Oxytocin not only increases eye contact and social bonding in humans but also exaggerates in-group favoritism. Adults given oxytocin are more likely to humanize in-group rather than out-group members by attributing human-unique emotions to the in-group members and showing increased positive evaluations of them (De Dreu et al. 2011). Men who are given oxytocin are three times more likely to donate money to their group rather than keep it for themselves (De Dreu et al. 2010). In economic games, intranasal oxytocin also reduces the likelihood of men to cooperate with out-group members when they become a threat to in-group members (De Dreu 2012, De Dreu et al. 2010, De Dreu & Kret 2016). Increased in-group bonds appear to drive larger defensive responses against potential threats from out-group members.

These results probably occur because of oxytocin's influence on the brain's social network, which allows for mentalizing and empathy. Immunohistochemistry suggests the presence of oxytocin receptors in the cingulate cortex and amygdala and perhaps even the frontal cortex (Boccia et al. 2013). Intranasal oxytocin also increases the resting-state connectivity between the amygdala and the mPFC (Sripada et al. 2013). This may cause a blunted mPFC response in individuals competing on behalf of in-group members against an out-group. Consistent with this idea, lower mPFC reactivity has been observed during competitions that increased people's willingness to harm out-group competitors (Cikara et al. 2014a). This is consistent with a subcortical system heavily impacted by serotonin and oxytocin, which both mediate the strength of the response in the brain's social cortex.

Selection for prosociality, which results in a reduced androgen profile and increases in serotonin (or receptor densities) as suggested by Cieri et al. (2014), is expected to facilitate oxytocin expression and binding (Baribeau & Anagnostou 2015). Sex steroids, including testosterone, affect the binding of oxytocin and vasopressin. Whereas testosterone facilitates vasopressin binding, oxytocin and testosterone are antagonistic. The production of oxytocin probably depends on serotonin receptor activity and generates a positive feedback loop, whereas serotonin increases in the presence of oxytocin.

The effects of oxytocin are mediated through serotonin neurons (Baribeau & Anagnostou 2015). This suggests that oxytocin's dependence on serotonin and interactions with testosterone altered its expression or reception over the past 80,000 years. The HSD predicts that the in-group bonds of our species coevolved with out-group distrust due to changes in the serotonergic and androgen systems that allowed oxytocin to have a greater impact on cortical regions related to social decision making.

Although intergroup lethal aggression is likely a conserved trait (Gomez et al. 2016, Wilson et al. 2014, Wrangham & Glowacki 2012, Wrangham et al. 2006), evolutionary modeling supports the idea that any intensification of out-group aggression could be a by-product of selection for intragroup prosociality late in human evolution. If each behavior evolves in isolation, the payoff is not as adaptive. If they emerge simultaneously, in-group favoritism in combination

with out-group hostility is a highly successful strategy (Choi & Bowles 2007). The interaction of oxytocin, serotonin, and testosterone suggests a way in which enhanced in-group prosociality and out-group aggression may have coevolved.

Ethnographic analysis also supports the idea that humans show a shift in social structure consistent with self-domestication and the coevolution of parochialism. Hunter-gatherers' intragroup interactions are best described as a reverse dominance hierarchy. Group members work together to defend each other against any individual trying to monopolize power in the group. This suggests that the most aggressive group members would be at a selective disadvantage. Aggression occurs, but ostracism and lethal aggression are levied against those who do not conform to the more egalitarian social system (Boehm et al. 1993). These bonded egalitarian groups would have been more successful in outcompeting other hominin species or human out-groups.

Humans became kinder and crueler as a result of selection for intragroup prosociality. Selection acted on neurohormonal channels that tune subcortical regions to be more or less reactive and subsequently influence the identity of those perceived as like us or not. Just as oxytocin bonds parent to offspring, making parents capable of extreme defensive aggression, our species became similarly protective of our in-group members against out-group threats.

Self-Control: The Unique Feature of Human Self-Domestication

Increases in brain size are the defining characteristic of evolution in our genus and a morphological signal of increased tolerance through self-control. Larger brains are associated with increased self-control. Self-control supports executive function and allows cortical regions to govern subcortical regions. The effects of self-control thus include inhibiting aggressive responses in favor of prosocial reactions (MacLean 2016). This effect contrasts with high or low subcortical reactivity that may sacrifice inhibition, as in bonobos and some dog populations (Bray et al. 2015, Wobber et al. 2010b).

A large-scale phylogenetic study (MacLean et al. 2014) suggests the relationship between brain size and self-control. An average of 15 individuals from 36 species of mammals and birds ($N > 550$) were tested for their ability to spontaneously inhibit a prepotent response in two different tasks. The first task presented subjects with food in a transparent tube. A correct response required inhibiting the urge to reach directly for the food and instead taking a detour by reaching through one of the tube's open ends. The second task gave subjects the Piagetian A not B task, which requires inhibiting perseverative search errors by choosing where food is hidden as opposed to where it was repeatedly hidden in the past.

Absolute brain size predicted performance across species. In more than 20 primate species, there was no link between performance and ecological variables such as social complexity or frugivory. Instead, brain size was the best predictor of inhibition. Brain size explained up to 70% of the variance in self-control across primate species (MacLean et al. 2014). This indicates that increases in absolute brain size in humans were likely accompanied by increases in self-control.

MacLean et al. (2014) suggest that the relationship between brain size and self-control in primates exists due to the unique scaling relationship between neuron densities in primates. Unlike other taxa, which show reduced neuron densities in larger-brained animals, primate neuron numbers scale isometrically with brain size. In primates, larger brains have the same densities of neurons, leading to exponential growth in potential networks between them (Azevedo et al. 2009). As the total number of neurons increase, primate brains become more modular, which may create new neural networks (Kaas 2000, Rilling et al. 2008b). Human brains take this primate trend to its extreme (Herculano-Houzel 2012). Thus brain size, neural numbers, and self-control can evolve as by-products of selection for body size (although see Grabowski et al. 2016). Simply becoming

larger to avoid predation or to promote thermoregulation would also increase self-control and trigger a positive evolutionary feedback loop during early human evolution (e.g., perhaps as seen between the small- and large-brained representatives of early *Homo*; Wood & Boyle 2016). Initial increases in self-control probably increased energetic productivity through more flexible solutions using ancient cognitive skills in new ways.

Cooking is a strong candidate for the initial trigger of this evolutionary feedback loop. Nonhuman apes prefer cooked food and have many of the cognitive prerequisites for cooking (Warneken & Rosati 2015, Wobber et al. 2008). A slight increase in self-control would have brought the energetic payoffs of cooking within reach (Wrangham 2009). Investing in expensive brain tissue would increasingly produce benefits as human energetic productivity expanded with more sophisticated cognitive abilities (Berbesque et al. 2016). These benefits would have led to the modern human energy budget, which is beyond anything seen in other primates. As a result, foragers would have higher reproductive rates and larger brains than any other ape (Pontzer et al. 2016). The cognitive by-product hypothesis is supported by fossil data interpreted to show brain size in our lineage scaling allometrically with body size until approximately 600 kya. According to this view, human brains became disproportionately large only in the last half million years (Hublin et al. 2015).

The HSD predicts that increases in self-control as a result of an increase in brain size steadily drove the evolution of tolerance and social cognitive skills. Late in human evolution, selection for in-group tolerance intensified and acted on our emotional axis, which, together with preexisting self-control, created unprecedented levels of social tolerance. Over the past 100,000 years, humans began to outcompete other hominins through the cooperation and communication that resulted from this increase in in-group bonding, tolerance, and cooperation.

Self-Domestication Through Evolutionary Development

It is important to consider the mechanism that selection might have targeted to produce these changes during human evolution. The HSD predicts that the evolution of developmental pathways is the unifying mechanism leading to the social cognition, temperament, and self-control that create unique human intragroup tolerance.

The widening of developmental windows is a common consequence of domestication. In domesticated animals, ancestral behavioral traits appear earlier and persist for longer (Trut et al. 2009). This heterochrony suggests that a similar shift in human development provided the mechanism for increases in tolerance and cooperative communication. Comparative and neurobiological work provides evidence of cognitive ontogeny consistent with the prediction that the human developmental window extended both earlier and later for cognition related to increased tolerance and cooperative communication.

Humans have unique early-emerging social cognition that facilitates participation in cultural forms of learning and is supported by a pattern of secondary altriciality and globular brain development. Longitudinal comparisons between age-matched human infants and nonhuman apes across a range of cognitive skills have revealed shifts in human cognitive development.

Wobber et al. (2014) published the first comparison that uses a longitudinal design to compare the cognitive development of two dozen bonobos and chimpanzees to a similar sample of age-matched children. Each subject was tested on the same battery of cognitive tasks each year between 2 and 4 years old. The battery was based on tasks used by Herrmann et al. (2007) and included social and nonsocial problem-solving tasks.

Contrary to models predicting slower cognitive development in humans relative to other ape species (e.g., Charnov & Berrigan 1993), 2-year-old children are more skilled than nonhuman

apes in social tasks requiring cooperation and communication. Performance in these tasks is near ceiling levels in humans by age 4, whereas the other apes show little development by this same age. The same 2-year-old human infants perform at a similar level to the other apes in nonsocial tasks (i.e., tool properties, numerosity, spatial memory, etc.).

This provides powerful evidence for specialized and early-emerging social cognition, which becomes the scaffolding for subsequent social learning in human infants (Herrmann et al. 2007). Early-emerging social skills allow human infants to cooperate and communicate with others and access all forms of cultural knowledge.

Fossil evidence provides a clue to when this early-emerging social neurocognitive network might have evolved. The most prominent feature of human brain maturation is secondary altriciality or helplessness in human newborns. Human brains are born at 25% their adult volume compared to other apes born with 45% of adult brain volume (Zollikofer & Ponce de Leon 2010). This extreme level of postpartum brain development gives unusual influence to social input during brain development (e.g., eye contact, motherese, etc.). Social interactions can influence the structure and organization of brain development during postnatal brain growth and probably facilitate the early-emerging social skills observed by Wobber et al. (2014).

Morphologically, the most unique feature of the human skull is its globular shape (Zollikofer & Ponce de Leon 2010). Analysis of globularization shows that this shape change occurs early in development and is largely a result of the maintenance of fetal brain growth rates until the eruption of the deciduous teeth at around 30 months old. By 4 years of age, synaptic densities begin to peak, the brain approaches adult size, and more than 60% of a child's metabolism is directed toward brain growth (Hublin et al. 2015, Kuzawa et al. 2014). The globular shape that is produced by the extension of exaggerated growth rates is largely driven by expansion in the brain's parietal region, which includes the PC and TPJ (Bruner et al. 2016, Gunz et al. 2012). This globular expansion is facilitated by elevated levels of white matter development in the human infant PFC relative to those of chimpanzees (Sakai et al. 2011). There is also evidence that the brain's cortical social network (i.e., the TPJ, STS, and mPFC) becomes increasingly active in infants during this period of globular brain development (Grossmann 2015). Globularization has also been linked to changes in the development of the neural crest as well as to a set of candidate genes that show signs of positive selection in humans (Benitez-Burraco et al. 2016).

All of the brain regions leading to globular expansion are also involved in human social cognition, including the attribution of mental states to others. This raises the possibility that globular growth in the fossil record signals the evolution of early-emerging social cognition.

Fossil studies have provided estimates for the appearance of secondary altriciality and globular brain development. In comparing the crania of infant *Homo erectus*, *H. neanderthalensis*, and *H. sapiens*, researchers have found that *H. erectus* infants were born with a more developed brain than those of later hominins. Secondary altriciality is thought to have evolved in the common ancestor of Neanderthals and modern humans. In contrast, globular development was not seen in *H. neanderthalensis*, suggesting that it is a unique feature of our species (Hublin et al. 2015). These studies support the idea of an early window of social cognitive development associated with a derived strategy of brain maturation that evolved uniquely in *H. sapiens*.

Although social cognitive skills develop early, synaptic pruning in cortical regions involved in executive function develops late. Human infants show similar levels of self-control to other apes until early childhood. It is not until around 6 years old that children show more inhibition than nonhuman apes (Herrmann et al. 2015, Vlamings et al. 2010).

Even adolescent humans have lower self-control than adults. Adolescents engage in higher-risk behaviors while showing greater aversion to social punishment (Casey & Caudle 2013). These trends are associated with the final stages of synaptic pruning in cortical regions thought to be

involved in executive control and inhibition (Casey 2015). Synaptic pruning in regions of the PFC related to self-control are only complete in our mid-20s. Only when these self-control networks are complete do adults become more risk averse and less sensitive to failure (Casey 2015). As the human brain increased in size, the process of synaptic pruning probably became increasingly pedomorphic. Brain myelination and white matter show a similar pattern of delayed development. Chimpanzees and macaques complete myelination at sexual maturity, but this same process is not complete in humans until our mid-20s (Somel et al. 2013).

Genetic comparisons also support the theory of a widened developmental window in humans. Comparisons of gene expression in macaques, chimpanzees, and humans reveal that a host of genes in humans are expressed at either an accelerated or delayed rate (Somel et al. 2009). The largest changes in the developmental timing of brain gene expression was observed in the human PFC as compared both to other areas of the human brain and to the chimpanzee PFC. Human synaptic genes in the PFC do not show peak expression until up to 5 years of age, whereas the peak for these same genes is reached after a few months in chimpanzees. This results in a late age for peak synaptic densities in the human PFC (3.5–10 years of age); in contrast, peak densities in the human auditory cortex occur between 6 months and 3.5 years of age, and synaptic elimination begins in the human visual cortex a few months after birth. This graded pattern contrasts with simultaneous peaks in all brain tissue types in macaques. The window of synaptic development is longer in humans because elimination begins later but occurs at a slower pace (Somel et al. 2013).

Research on self-control and synaptic pruning is consistent with an increased window of development in humans as predicted by self-domestication. The HSD predicts that both early-emerging social cognition and delayed adult inhibition will be linked to selection for prosociality and provide a mechanistic explanation for features of HSD.

CONCLUSION

Researchers have frequently made use of the concept of domestication in explaining human evolution (Boas 1911, Gould 1977, Leach 2003, Wrangham 2014). Darwin (1859) began *On the Origin of Species* with a discussion of domestication through artificial selection and spent decades collecting examples of natural variation produced through domestication (Darwin 1868). Domestication was crucial to Darwin's case for evolution through natural selection and led him to consider the possibility of human domestication (Darwin 1871).

It was not until the pioneering work of Dmitry Belyeav and colleagues that the HSD, or the link between selection for prosociality and a wide variety of correlated by-products, was discovered (for a review, see Hare & Woods 2013). These by-products include morphological and physiological changes, increases in cooperative communication, and expanding developmental windows (Belyaev et al. 1985, Hare et al. 2005). Belyaev's experimental domestication of foxes clearly defined the selection pressure, its effects, and the potential developmental mechanisms targeted to produce different domesticated phenotypes. The fox experiments allowed further comparative work to test whether natural selection produced similar results in dogs, bonobos, and humans.

The experiments with foxes and comparisons between dogs and wolves reveal that changes in cooperative-communicative abilities can occur as a by-product of selection for prosociality and against fear and aggression. A priori tests of bonobo self-domestication support the possibility that natural selection causes similar results.

The HSD builds on this comparative work and suggests that selection for prosociality also played a large role in human evolution, especially during the Middle and Upper Paleolithic (**Figure 1**). The first a priori test of this hypothesis found evidence by the Upper Paleolithic for the expected link between increases in cultural artifacts and craniofacial signals of increased tolerance.

Future tests can evaluate the proposed link between the evolution of self-control and emotional reactivity that allows flexible human tolerance and social cognition. Future paleoanthropological, neuroendocrine, and genetic research will be able to further examine links between intragroup cooperative communication, morphology (i.e., eye color), and heterochronic shifts related to early-emerging social cognitive development. Hopefully, the HSD will help energize efforts toward answering the ultimate Darwinian challenge: how our minds evolved and allowed *H. sapiens* to survive as Earth's last remaining human.

SUMMARY POINTS

1. Darwin's greatest evolutionary challenge is identifying derived forms of human cognition and the processes by which they evolved. Given recent evidence of the existence of many large-brained human species within the past 50,000 years, we must answer this challenge for both our genus and our species.
2. Comparisons between human and nonhuman ape infants suggest that the early emergence of cooperative communication provides the developmental foundation for human cultural cognition.
3. Domestic dogs converge with human infants in their ability to use human cooperative-communicative gestures. Experimentally domesticated fox kits show dog-like skills in using human gestures even though these skills were not under selection. An increase in cooperative-communicative ability appears to be a by-product of selection for prosociality over aggression.
4. Comparisons between bonobos and chimpanzees support the hypothesis that natural selection favoring prosociality over aggression can lead to self-domestication. Bonobos share many traits with domesticated animals, including increased flexibility in some cooperative-communicative contexts.
5. The HSD suggests that natural selection for prosociality and against aggression played a large role in human evolution. Over the past 80,000 years, fossil humans show morphological evidence for selection against aggression that coincides with an increase in cultural artifacts in the fossil record.
6. Selection for in-group prosociality drove human self-domestication in the Paleolithic. Changes in oxytocin and eye sclera color provide two possible mechanisms to explain the increases in cooperative communication, increases in in-group cooperation, and intensification of intergroup conflict that evolved as a result of this selection.
7. Evolutionarily labile neurohormones and neuropeptides provide a ready target of selection for prosociality over aggression. However, human tolerance is flexible beyond what can be accounted for by muted subcortical responses alone. Phylogenetic comparisons suggesting a strong link between inhibition and absolute brain size point to the critical role of cortical regions in allowing for human levels of self-control and tolerance.
8. Human self-domestication predicts increased developmental windows for traits relating to increased tolerance and cooperative communication. Early-emerging social cognition, which develops despite secondary altriciality, together with graded synaptic pruning continuing into adulthood, played a central role in the evolution of *H. sapiens*.

FUTURE ISSUES

1. The HSD predicts a strong link between individual differences in temperamental profile and mentalizing abilities. Future studies should continue to find evidence for this relationship early in development, using studies of heritability and cross-cultural comparisons.
2. Self-domestication predicts the appearance of the domestication syndrome, but its expression likely differs across taxa due to phylogenetic distance and different developmental, neurohormonal, or subcortical targets. Traits considered part of the syndrome do not present themselves universally (Sanchez-Villagra et al. 2016). This inconsistent pattern may be the result of multiple pathways to increased prosociality, each of which may generate different sets of correlated by-products. For example, humans and bonobos are hypothesized to be self-domesticated, but humans exhibit lethal aggression and neither hominoid shows the high frequencies of piebalding seen in many other domestic mammals (Wilkins et al. 2014). Tools will be needed to discriminate between selection against different forms of aggression (i.e., defensive, predatory, intragroup, intergroup, etc.) that affect different physiological or developmental mechanisms and may lead to this differential expression of correlated traits (Hare et al. 2012). Future selection experiments that target different forms of aggression or prosociality will provide powerful tests (Sanchez-Villagra et al. 2016).
3. The HSD suggests that the underlying evolutionary genetics behind human white sclera can potentially reveal the time of origin for human forms of cooperative communication (Tomasello et al. 2007). For example, if genetic disorders related to sclera color are discovered, then this could provide a powerful test of the self-domestication hypothesis using comparisons of the human and Neanderthal genomes. Individual variability in scleral whiteness in nonhuman apes may offer another route to genetic clues about the origin of human sclera coloration (Mayhew & Gómez 2015).
4. The HSD predicts that *H. sapiens* have an expanded developmental window. Morphological comparisons of development in *Homo* are based on a few fossil specimens. Future discoveries of additional specimens should support extended fetal levels of brain growth and cranial globularization as well as a slower life history in *H. sapiens*, which would support the hypothesis of gradation in brain development across cortical levels (i.e., late myelination and pruning of the cortex).
5. Selection for prosociality is only associated with reduced rather than increased brain size. Another major force, or multiple forces, must have been at play during early human evolution to drive initial body and brain size increases. Increases in body size to escape predation or better thermoregulate or as a result of the island syndrome may have initially produced tolerance as a by-product of self-control increases occurring with concomitant changes in brain size. Selection could then target any heritable variance in self-control. This alone may be the cognitive trait allowing for an initial shift in human energy productivity (Pontzer et al. 2016). Comparative behavioral ecological studies will likely help test whether similar evolutionary scenarios have played out in other taxa.

6. The cooperative breeding hypothesis might be considered an alternative hypothesis to the HSD (Burkart & van Schaik 2010). Although the two hypotheses will likely prove complementary, it will be important to outline and test their competing predictions (ideally using comparative phylogenetic techniques). For example, cooperative breeding does not make the heterochronic or morphological predictions made by the HSD, but both hypotheses predict increased prosociality. Therefore, the hypotheses might be reconciled. For example, it is conceivable that increases in cooperative breeding during human evolution might have led to sexual selection. Females may have chosen to bond with males who did not aggress toward them but rather toward threats to their joint offspring—leading to human self-domestication.
7. Self-domestication is predicted to play a role in shaping the phenotypes of both island- and urban-living populations (Ditchkoff et al. 2006, Raia et al. 2010). Careful comparisons of island and mainland as well as wild and urban populations will help reveal the ecological conditions that favor self-domestication. These lessons will likely also allow for inferences regarding the ecological conditions that favored human self-domestication.
8. If selection acts on prosociality across a variety of species, shared genetics might produce the observed convergence across some species. Any common genetics discovered could be evaluated in extinct and living humans. This would require genotypic and phenotypic comparisons of different pairs of wild and domestic animals, but initial attempts have not revealed this type of commonality (Albert et al. 2012). Future research can explore new genetic candidates related to neural crest development, cranial globularization, and domestication that might be associated with human self-domestication (Benitez-Burraco et al. 2016). However, the human case may prove exceptionally challenging because human behavioral traits are hyperpolygenic (Chabris et al. 2015).

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

I want to thank Richard Wrangham for making the connection between the dog domestication literature and hominoid evolution, both in the case of humans and bonobos. His ideas, discussions, and collaboration inspired this review. I also want to thank James Brooks for help with the reference section and Steve Churchill, Evan MacLean, Jingzhi Tan, Michael Tomasello, Vanessa Woods, and Richard Wrangham for extremely valuable comments that resulted in a much-improved paper.

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