What role have humans played in modifying animal behaviour? A case study of the domestic dog

ABSTRACT

The role of humans in shaping the behaviour of modern dogs is striking. Modern dog breeds, having arisen through extensive artificial selection, number in the hundreds and all have distinctive behavioural characteristics. However, the role humans have played in the original behavioural modifications that occurred during the domestication of grey wolves and the origin of the domestic dog are much less clear. How did dogs become tame? How did they develop the ability to follow human commands and cues? What genetic changes may have occurred during this process? And crucially, what role did humans play in this process? This essay explored the role of humans in altering behaviour during the early domestication of dogs by drawing together current theories from three key areas of research; the origins of dog domestication, models for behavioural modification and the genetic basis for behavioural change. These areas of research have shed new light on the behavioural origins of the domestic dog, reassessing the role of humans dramatically from an active force, purposefully domesticating dogs and altering their behaviour, to an environmental factor that the dogs themselves adapted to. In addition to this, research into behavioural traits of dogs, phylogeny of domestication and genetics of behaviour suggests that early dogs evolved cognitive behavioural skills that allowed them to read human body language and adapt to human social environments and that selection for genes conferring tame behaviour were key in driving the domestication of dogs from their wild ancestors. When drawn together, this broad range of research spanning over fifty years, challenges the long held romantic images of savage beasts coming in from the cold to sit round mans fire and instead paints a far more complex and fascinating picture of the role of humans in behavioural change and domestication of the dog.

INTRODUCTION

Humans use animals for livestock, transport, materials, performing tasks and companionship. These relationships have stemmed from domestication, human manipulation of animal behavioural and morphological phenotypes by artificial selection to accentuate and preserve genetic characteristics across generations that are favourable or appealing to humans (Darwin 1859; Rindos 1984; Clutton-Brock 1992). The domestication of animals, along with crop plants, to form agriculture has been crucial to the development of human society and allowed the development of settlements and subsequently the founding of civilisations (Diamond 2002). Although livestock animals such as sheep, cows and pigs are arguably the most important of the animal species that have been domesticated by humans as they are a major source of food and resources (Clutton-Brock 1981; Smith 1998), the oldest domesticated species and one of the most compelling examples of behavioural modification by humans is the domestic dog (*Canis familiaris*), domesticated from grey wolves (*Canis lupus*) (Crockford 2000; Acland & Ostrander 2003; Galibert et al. 2011). The significant role of humans in the modification of behaviour in modern dog breeds is clear, extensive selective breeding has resulted in a vast array of behavioural traits amongst dog breeds (Coppinger & Scheider 1995; Ostrander et al. 2006; Spady & Ostrander 2008). Herding breeds for example express strong predatory linked

behaviours and are adept at responding to complex ranges of human cues such as whistling and vocalisations to instruct them during herding (Coppinger & Scheider 1995; Galibert et al. 2011). However how did dogs originally develop the ability to follow human commands? In comparison to our knowledge of selective breeding in modern dog breeds, much less is known about the role humans have played in the original behavioural modifications that occurred during the domestication of grey wolves and the origin of the domestic dog. This essay aims to explore the role humans have played in the initial modifications of dog behaviour that accompanied domestication, highlighting current theories surrounding how domestication of dogs occurred, the behavioural changes that accompanied early domestication and the potential mechanisms involved in such behavioural changes.

DISCUSSION

The Origin of the Dog

The origin of the domestic dog is a highly contested and controversial topic, with the location of domestication and date at which it occurred being areas of much debate. Different research groups put the date of domestication as far apart as 12,000 and 33,000 years ago (Davis & Valla 1978; Pang et al. 2009; Ovdov et al. 2011; Wang et al, 2013) and the location of dog domestication in regions as varied as East/Southeat Asia (Savolainen et al. 2002; Pang et al. 2009; Wang et al. 2013), Central and Eastern Europe (Germonpré et al. 2009) and the Middle East (Davis & Valla 1978; Von Holdt et al. 2010; Axelsson et al. 2013). Further debate surrounds theories regarding whether or not the domestic dog stemmed from a single lineage of grey wolf (Pang et al. 2009; Von Holdt et al. 2010) or several lineages independently with various source populations (Germonpré et al. 2009; Ovod et al. 2011), whilst one recent study suggests a divergence of dogs then continued 'backcrossing' with different lineages of wolf throughout history (Freedman et al. 2014). Whenever and wherever it did occur, the domestication of wild wolves had profound effects on wolf behavioural and morphological traits, which resulted in speciation from wolves to domestic dogs. (Clutton-Brock, 2006; Germonpré et al. 2009). From a behavioural standpoint, the changes were vast and offer one of the most compelling examples of the role humans can have in modifying animal behaviour.

The Origin of Human-Wolf Interactions and Early Behavioural Modifications

The manner in which the domestication process of wolves started is still, and may always be, unknown, although two theories 'adoption' and 'self-domestication' are the most commonly proposed. The adoption theory posits that humans adopted wolf cubs and integrated them into their social circles, using tamed wolves for hunting and eventually domesticating them (Muller 2002). However this theory receives criticism in being historically anthropocentric in its assumption that humans intended to actively domesticate dogs, despite having no existing model of domestication to influence them or draw upon (Morey 1994). Further criticism is drawn from the fact that tamed wolves show no predisposition to share food, can be dangerous upon reaching sexual maturity and may have been a predatory species to humans and therefore avoided, although the latter point is still contested (Koler-Matznick 2002; Clutton-Brock 2006).

The self-domestication centres on a theory of proto-domestication through gradual behavioural changes in wolves as a process of natural selection, influenced by human-wolf interactions, which would have later been followed by artificial selection by humans (Coppinger & Coppinger 2001; Ortolani et al. 2009). The theory posits that some wolves may have been attracted to food refuse in and around human settlements. While humans are likely to have chased away or killed wolves that were unafraid of humans and aggressive, they may have been more tolerant of individuals that were unafraid of humans enough to approach their settlements but showed no aggressive or threatening behaviour (Crockford 2000; Coppinger & Coppinger 2001; Driscoll et al. 2009). This allowed access to a new food source and thus bold and non-aggressive, perhaps even 'friendly' behaviour in wolves gained a significant fitness advantage in populations interacting with human settlements. In short, humans may have initially passively modified the behaviour of wolves through the wolves' interaction with the human environment and the fitness advantages they gained from being able to access it through exhibiting tame behavioural traits (Driscoll et al. 2009). After these behavioural changes through natural selection, tame 'proto-dogs' that interacted comfortably with humans may have been incorporated into human society and selected for particularly beneficial traits that aided hunting efficiency and settlement guarding, thus beginning full domestication (Coppinger & Coppinger 2001; Driscoll et al. 2009; Driscoll & Macdonald 2010).

The Behavioural Consequences of Domestication: Tameness and Social Cognition Behaviour

As previously established, the domestication of dogs from wolves brought on profound behavioural changes, particularly in fear and aggression. When comparing behaviour between modern day domestic dogs and wolves, social tolerance, and friendliness persists, compared to wolves, dogs are docile, and eager for human contact (Copinger & Copinger 2001; Driscoll & Macdonald 2010)

In addition to this tame behaviour, dogs have developed novel social cognitive mechanisms that mirror those found in humans and allow dogs to read and respond to human social cues in a way not exhibited in wolves or even non-human primates such as chimpanzees (Povinelli et al. 1997; Hare & Tomasello 2005). Dogs are able to respond to human gestures and eye movements to solve tasks such as finding a hidden food item; similar to skills that are exhibited in human infants at around 14 months (Hare et al. 1998; Miklósi et al. 1998; Behne et al. 2005; Lakatos et al. 2009). To determine whether this behaviour is learned or an inherited trait in dogs, experiments where carried out on dog pups with no prior socialisation to humans. The experiments found that the pups scored highly on all tests, indicating that such behavioural skills are inherited (Hare et al. 2002; Miklósi et al. 2003). Wolf pups, when tested, did not exhibit such behaviour (Hare et al. 2002; Miklósi et al. 2003). However, experiments with adult wolves and chimpanzees found that they are able to learn these skills after extensive human socialisation and teaching although they are still outperformed by dogs (Call & Tomasello 1996; Miklósi et al. 2003; Virányi et al. 2008).

These experiments indicate that although the ability to read human behavioural cues does not occur naturally in wolves or chimpanzees, the potential to develop this behaviour is present (Hare & Tomasello 2005). In non-social interactions however, dogs do not exhibit particular adeptness at performing tasks compared to other animals (Frank et al. 1989; Osthaus et al. 2005). This suggests that dogs have developed cognition skills that are specifically tailored to social interaction with humans. The fact that human infants and dogs share very similar social behaviour skills that occur without entraining and are not found in the most closely related wild relatives of either species suggests that these types of social cognition behaviours have evolved independently in both humans and dogs, specifically in response to sustained social interaction with humans (Miklósi et al. 2004; Hare & Tomasello 2005; Kubinyi et al. 2007; Gácsi et al. 2009).

A Possible Model for Behavioural Changes in Dogs Through Domestication: The Fox Farm Study

Although it is not known exactly how interaction with humans led to decreased aggression and the development of social cognition behaviours in dogs, one seminal study offers the most compelling model for the modification of behaviour in canids under domestication by humans. In the 1950s, Russian geneticist Dmitry Belyaev began a program to investigate the potential processes that may have occurred in the domestication of the dog, using the silver fox (*Vulpes vulpes*) a canid species that had been bred in captivity for fur farming but never domesticated (Trut 1999). Belyaev hypothesised that the selection of heritable behavioural traits rather than morphological traits was responsible for domestication. It was predicted that the selection for non-aggressive and non-fearful responses to humans would result in a domesticated population of silver fox (Trut 1999).

Selection for mating was based strictly on the behaviour of the foxes. Individuals that showed fear and aggression to human handlers approaching their cage were not selected for breeding whilst individuals that were less timid and did not act aggressively were selected. The same sectional process was carried out on each generation of fox pups to select for the tamest individuals (Trut et al. 2004). In addition to this, control groups where no behavioural traits were selected for and where aggressive traits were selected for where created (Trut 1999). To ensure any behavioural changes that occurred were genetically heritable rather than effects of epigenetic, maternal or human environmental influences; all human interaction was limited to strict time periods, cross breeding and cross-upbringing of pups between tame, aggressive and non-selected for mothers was carried out and transfer of tame embryos to non-selected for and aggressive mothers and vice versa was practiced (Trut et al. 2009).

Selection for tameness across generations led to the development of behavioural and morphological changes similar to the differences seen between dogs and wolves (Belyaev et al. 1985; Trut 1999). Behaviourally, individuals became less aggressive, sought out human contact, playful behaviour persisted into adulthood and dog like tendencies towards humans such as licking, whining and tail wagging were displayed. Morphologically, individuals developed floppier ears, a greater array of tail shapes, a greater array of coat markings and colouration, lost seasonal breeding cycles and exhibited

altered skull, teeth and jaw structure, all differences in morphological traits that are found between dogs and wolves (Trut 1999; Trut et al. 2009; Kukekova et al. 2012). Perhaps most strikingly from a behavioural perspective: tame foxes also exhibited similar cognitive behavioural skills to those found in dogs, despite these skills not having been selected for at all (Trut et al. 2004; Hare et al. 2005; Kukekova et al. 2012). For example, tame foxes were able to follow human cues as well as developing communicative vocal and physical cues of their own to interact with humans (Hare et al. 2005; Gogoleva et al. 2011). Fox pups bred for tameness performed just as well as dog pups in tests measuring the ability to read human gestures to find hidden food. Crucially, fox pups bred for tameness greatly outperformed fox pups from lineages not selected for any behavioural traits (Hare et al. 2005). Interestingly, this combination of physical and behavioural changes has been found consistently in studies comparing various groups of domesticated animals to closely related non-domestic species, a pattern that has been termed as 'the domestication syndrome' (Hare et al. 2012). Hare et al. compiled data from studies comparing a range of traits (aggression, physiology, morphology, prosocial behaviour, delay in development and cognition) between domestic and wild animal counterparts: dogs and wolves, silver foxes and wild foxes and domestic guinea pigs and wild guinea pigs (cavies). Bonobos and chimpanzees were included in the study as although bonobos are not strictly domesticated, they exhibit a range of traits that are reminiscent of domestic behaviours that are unique amongst non-human apes and may represent an example of self domestication through social pressures selecting for non-aggressive behaviour. However this theory is still under much debate and still requires further research (Hare et al., 2012). All domesticated species compared have been found to exhibit specific analogous phenotypic patterns: reduced aggression, reduced stress responses, reduced cranial capacity, depigmentation of coat, increased playful and sexual behaviour, delayed fear response, retention of juvenile communicative traits into adulthood and increased cognitive problem solving abilities. Dogs and silver foxes also exhibited reduced canine dimorphism and increased sensitivity to human social cues (Hare et al. 2012).

The findings of these studies suggest that selection on systems controlling fearful and aggressive behaviour correlates with the altered activity of a specific set of regulatory genes. These changes could have been key in the domestication of dogs and may have led to the behavioural changes we see between wolves and dogs today, including differences in social cognition behaviour which may have arisen as a result of fear and aggression selection rather than being selected for directly.

Potential Mechanisms of Behavioural Modification

The next stage of the fox farm experiments has been to identify the specific underlying causes of the observed behavioural changes. Behavioural changes have been attributed to significant differences in hormones, steroids and neurotransmitters that occur between tame and control foxes (Gulevich et al. 2004; Kukekova et al. 2012). For example compared to control foxes, tame foxes exhibit lower densities of 5-HTA1 serotonin receptors in the hypothalamus and higher levels of serotonin in the midbrain (Popova 1997). At a genetic level, studies are currently trying to determine genetic loci that are linked to specific behavioural traits (Kukekova et al. 2011a, 2011b, 2012). Replicate studies

selecting for tameness have also been carried out on groups of rats in the hope of identifying similar loci responsible for behaviour changes to determine how well conserved they are across species (Albert et al. 2009). Comparative studies between tame fox and rat genomes have so far found the conservation of behavioural loci encoding for individuals touching human hands when approached and allowing their stomachs to be touched by humans (Albert et al. 2009; Kukekova et al. 2012). Subsequently, these loci have also been found in dogs (Von Holdt et al. 2010), further suggesting that similar selectional pressures on behaviour may have been present in early domestication.

SYNTHESIS AND CONCLUSIONS

Research into the origins of dog domestication, the potential models for behavioural modification and the genetic pathways involved have, and will continue to, shed light on the background of behavioural changes in dogs from wolves.

Currently, studies in the potential genetic pathways behind behavioural changes, initially studied in the fox farm experiments offer the most exciting route for further understanding the modification of behaviour in domestic dogs. Further identification of genes responsible for behavioural changes and the complete mapping out of their genetic pathways is a crucial next step for further understanding behavioural modification. Although comparative studies have found the conservation of gene loci encoding for tame behavioural traits in foxes, rats and dogs, comparative studies in dogs and wolves for differences in the presence of these loci are necessary to further help to determine whether behavioural modification in dogs occurred through selection for tameness. If differences in tame behaviour encoding loci are found between wolves and dogs, future experiments could carry out genomic comparisons on ancient dog bone samples to identify the point at which particular behaviour changes occurred. A model study would be a recent investigation (Axelsson et al. 2013) that has discovered the presence of a starch-digesting enzyme in the genome of early dog bone samples coinciding with the development of agriculture. Similar studies could be carried out in this manner, looking for the presence of specific behaviour genes in early dogs to identify the beginnings of behavioural modification.

Although it may eventually be possible to determine the exact genetic causes of the differences in behaviour between wolves and domestic dogs, we will never be able to truly understand the role humans played in these changes. All theories on early domestication remain precisely that, theories, and are likely vast simplifications of what may have been an incredibly complex and dynamic process. However, despite not understanding the specific processes involved it is clear that early domestication of dogs involved human interaction. On that basis alone, regardless of whether it was active, completely passive or something much more complex, the role of humans in the modification of dog behaviour through domestication has been profound.

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