Dog faces exhibit anatomical differences in comparison to other domestic animals

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Faces and their movements provide us the ability to understand parts of the evolution of communication, social behavior, cognition, and the brain (Schmidt & Cohn, 2001; Parr & Waller, 2006; Burrows, 2008). Humans and other mammals communicate using numerous signals that include visual displays, vocalizations, tactile signals, and olfactory signals (Burrows, 2008; Brecht & Freiwald, 2012; Liebal *et al.*, 2013). Each of these signals is generated or received at least partially using the craniofacial complex. Within the visual realm, the face is the primary communication tool for terrestrial mammals and this is where facial expressions are generated. Many mammals also have facial fur of contrasting patterns and colors that are themselves used as a kind of signaling in social interactions (Santana *et al.*, 2012, 2013; Caro *et al.*, 2017). Human (and most mammalian) faces make facial expressions using the numerous mimetic muscles found deep to and attached to the skin of the face. These facial expressions help individuals with cohesion of social and kin groups, maintaining relationships, and potentially signal the intent and emotional state of the sender (Parr & de Waal, 1999; Parr & Waller, 2006; Burrows, 2008; Burrows & Cohn, 2014). A large majority of these studies comes from primates but recent work has increased our understanding of how some domestic mammals use facial expression in social interactions with conspecifics and humans (Wathan *et al.*, 2015; Caeiro *et al.*, 2017; Kaminski *et al.*, 2017; Maglieri *et al.*, 2020; Waller *et al.*, 2020).

Because facial expressions and mimetic muscles are associated with social groups, complexity of social interactions, and the cognitive/neural networks that manage these interactions, they are of interest to people studying the evolution of social behavior and the brain within ourselves, primates, and all other mammals.

All mammals have mimetic muscles which, with the likely exception of cetaceans (dolphins, porpoises, and whales), generate facial expressions. Ethograms (catalogs of behavior observed in any given animal) from a wide variety of mammals demonstrate the use of facial expressions in short-distance social interactions, but the majority of these are exclusive to primate species.

While primates have occupied much of in the research literature, recent work has begun turning to domestic mammals; their faces, mimetic muscles, and facial expressions. Humans are the only living species that have domesticated other species for our own interests. Studying our closest living relatives, the chimpanzees and bonobos, can inform our understanding of how our own social behavior, cognition, and brains evolved, but what a gaping hole we leave in that understanding by missing the very species that we have created!

Domestication involves multiple processes but it occurs quickly, relative to the descent of new wild species (*e.g.*, Darwin, 1859, 1868; Larson & Fuller, 2014). Archeological and molecular evidence indicates that humans started bringing wild animals “into the fold” around 30,000 years ago with domestication of the dog from gray wolves (Driscoll *et al.*, 2009; Ovodov *et al.*, 2011; Druzhkova *et al.*, 2013). The specific population(s) of gray wolves that gave rise to domestic dogs is now extinct but this process that began in the Late Pleistocene seems to have occurred relatively simultaneously in Western Europe, East Asia, and Central Asia and pre-dates the dawn of agriculture in these areas (Vila *et al.*, 1997; Clutton-Brock, 1995, 1999; Frantz *et al.*, 2016). Domestication of other mammals followed much later than dogs and includes goats, horses, and cats, among others, beginning around 10,000 years ago (*e.g.*, Driscoll *et al.*, 2009) .

Domestication of mammals generally results in new species that are distinguished both

morphologically and behaviorally from their closely related wild counterparts as well as their ancestors (see Box 1). Domesticated mammals typically display a suite of morphological, physiological, and behavioral traits that are unique relative to their wild ancestors and counterparts and this phenomenon is sometimes referred to as the “domestication syndrome” (Wilkins *et al.*, 2014). Primary among these is decreased aggression, changes in pelage (coat) color and pattern, decreased size of the midface (snout) and teeth, ears that are floppy (with some notable exception), and a generally more gracile craniofacial complex (Darwin, 1859, 1868; Larson & Fuller, 2014; Wilkins *et al.*, 2014). Something about the *process* of domestication, across the wide phylogenetic range of animals, results in this generalized suite of characteristics. Several recent studies have pointed to neural crest cells, a group of stem cells peculiar to vertebrate animals, as being the common shared developmental connection in this “domestication syndrome”, from fish to birds to dogs.

Increasing our understanding of the anatomical and behavioral differences between domestic mammals and their wild counterparts/ancestors can also inform our understanding of what humans thought was valuable in the domestication process as well as how humans and domestic mammals communicate with one another via facial expression. It may also help us understand our own “self-domestication”, the progressive set of domestication syndrome traits increasingly present throughout human history, including reducing body mass, shortening of the midface and tooth size, reduction in aggressive behavior, and reduction of sexual dimorphism (*e.g.*, Hare, 2017; Wilkins, 2017; Hare, 2017; Wrangham, 2019).

Box 1 with Figure 1: Domestication of wild mammals into new species occurred across the world but generally has resulted in species that have more variations in pelage color and pattern, reduced craniofacial robusticity, and increased docility. While many mammals have been domesticated, Figure 1 illustrates three domestic mammals that are familiar to many people. Top row left to right: domestic cat (*Felis catus*) and its direct, wild ancestor the African wild cat (*F. silvestris libyca*); Middle row left to right: domestic horse (*Equus caballus*)

and its close, wild relative Przewalski's horse (*E. przewalskii*) Bottom row left to right: domestic dog (*Canis familiaris*) and its close, wild relative the gray wolf (*C. lupus*).

Domestic cats are only marginally different from the African wild cat in terms of morphology and behavior (Driscoll *et al.*, 2007, 2009). In these images, both the domestic and wild cat appear relatively similar in terms of craniofacial morphology and are both relatively solitary by nature.

The domestic horse is closely related to the wild Przewalski's horse but important facial differences are obvious here. The domestic horse generally has a more gracile head, greater variation in pelage pattern, and a change to a flat mane from the erect mane in Przewalski's horse. While studies of Przewalski's horse in the wild are incomplete, their behavior seems to parallel that of feral domestic horses, with both species being social animals (Boyd, 1988; Feh, 2005; Orlando *et al.*, 2013).

The domestic dog (*Canis familiaris*) differs overtly from its close wild relative, the gray wolf (*C. lupus*). Unlike the cat, dogs have an explicitly different suite of anatomical and behavioral characteristics relative to the gray wolf which include smaller vibrissae (or whiskers), external ears that are typically floppy in most breeds, more gracile craniofacial complex, and overtly affiliative behaviors toward humans. Holding eye gaze has become one of the hallmark features of the relationships between humans and domestic dogs (Miklosi *et al.*, 2003).

All figures in the left column from the first author, all figures in the right column from Pixabay (free share images at www.pixabay.com).

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Horses, cats, and dogs all use facial expressions in their interactions with humans but to varying degrees. While equivocal, accumulating evidence is demonstrating that humans and dogs are uniquely attuned to one another's facial expressions to the exclusion of other domestic mammals (Schirmer *et al.*, 2013; Waller *et al.*, 2013; Albuquerque *et al.*, 2016). Not only are humans good at reading facial expressions of dogs, but dogs are good at reading facial expressions of humans (*e.g.*, Correira-Caeiro *et al.*, 2020). Does this mutual ability to read one another's facial expressions indicate that dogs and humans co-evolved and influenced one another's brain evolution? Cats typically do not recognize the face of their human handlers by way of visual cues, as opposed to the situation in dogs, but they do recognize faces of other cats (Lomber & Cornwell, 2005). Other studies have suggested that cats are not particularly responsive to their owners' faces and that people are not as good at reading cat facial expressions as dogs (Bennett *et al.*, 2017; Galvan & Vonk, 2015). Explanations for these phenomena focus on several areas, including the evolution of dogs from an already highly social canid ancestor while cats evolved from a less social felid ancestor, as well as the longer time frame that humans and dogs have lived together.

Emerging evidence is showing that domestic horses are able to read some aspects of both other horses' and human facial expressions but evidence for humans being able to accurately read horse facial expression is not yet as compelling (Proops & McComb, 2012; Proops *et al.*, 2009, 2018; Smith *et al.*, 2016; Wathan *et al.*, 2016). Horses themselves are social animals, both in domesticated and feral settings and, due to their social natures, may attend to facial expressions (Smith *et al.*, 2016; Proops *et al.*, 2018).

Horses, be they domestic horses, feral horses, or Przewalski's horses, are diurnal and rarely solitary by nature. *E. przewalskii* is endangered in the wild but several robust field studies of their social behavior have been conducted, showing that this species is highly social and occurs in herds that number from 9 individuals-23. However, almost certainly these numbers are limited by the few numbers of these horses in existence (Boyd, 1988; Wolter, 2018). Social groups include both harems and bachelor male groups. Aggression in *E. przewalskii* is suggested to be high (e.g., Feh, 1988), but social groups form long-lasting bonds that remain in close proximity to one another and members of harem herds spend considerable time grooming one another. Przewalski's horse is smaller than most breeds of domestic horse, which may reflect the traits human chose during domestication that focused on using horses for transportation.

Feral groups of domestic horses have similar social behavior (e.g., Klingel, 1982; Cameron *et al.*, 2009). Social communication includes many of the same signals used by domestic horses, including olfactory communication, short-distance vocalizations, and facial expressions including movements of the ears and eye region. Domestication of the horse seems to have begun around 4000BCE in Mesopotamia and China in association with their use as a transport animal. There are now more than 400 domestic breeds. Contemporary horses generally bear a more neotenous set of characteristics than seen in Przewalski's horse and other wild equids. While fur on domestic horse faces comes in a variety of colors and patterns, the general form of the skull does not differ markedly from that of wild equids.

Recently developed Facial Action Coding System for horses (EquiFACS) has shown that domestic horses have a complex and high number of facial expressions that they display in

interactions with one another and with humans (Wathan *et al.*, 2015). Given that both feral and Przewalski's horses have complex social behavior and live in life-long socially bonded groups, it is not surprising that they have a complex facial expression repertoire.

Domestic cats represent a vastly different scenario. The cat (*F. catus*) appears to have first been domesticated somewhere in the Fertile Crescent around 4,000 years ago during the Near East Neolithic period. The image on the right of the African wild cat (*F. silvestris lybica*) is the ancestor of all domestic cats. Domestication of the cat has resulted in only minimal anatomic and behavioral differences relative to the African wild cat to the extent that the domestic cat is sometimes considered to be a subspecies of *Felis silvestris*: *F. s. catus* (e.g., Randi & Ragni, 1991; Clutton-Brock, 1999; Driscoll *et al.*, 2009). One of the only ways to grossly differentiate the domestic cat from the African wild cat is pelage color, with the wild cat typically varying little in the range of pelage coloration and patterning. Domestic cats, like the domestic horse, display a wide variety of coat colors. Associations between humans and wild cats probably were commensal, with cats feeding on rodents that infested grain stores of the earliest farmers.

Domestic cats can be remarkably affiliative with humans but they do not have the range of facial expressions seen in domestic horses or in domestic dogs. CatFACS is a Facial Action Coding System developed to quantify and describe cat facial expression and this system has demonstrated a lower number of facial displays relative to horses and dogs (Caiero *et al.*, 2017). Many cat facial expressions are focused on movement of the ears and changes in the size and shape of the pupils (Bennett *et al.*, 2017; Caiero *et al.*, 2017) and, unlike in dogs, cat facial expression is not correlated to how quickly humans adopt cats from cat shelters (Caiero

et al., 2017). Cat facial expressions do not appear to have undergone the selection that dogs underwent during the domestication process.

All felids are relatively solitary, predatory mammals, with the exception of the African lion (*Panthera leo*), and domestic cats do not diverge from this general characteristic. Most wild felids are either primarily nocturnal or crepuscular (active at dawn and dusk), with the exception of the cheetah (*Acinonyx jubatus*). Unlike the wild equids and wild gray wolves that gave rise to domestic horses and domestic dogs, the African wild cat (*Felis silvestris lybica*) is asocial and, therefore, probably does not have a complex or numerous facial display repertoire that could have served as a basis for domestic cats.

Domestic dogs (*Canis familiaris*), unlike cats, bear far less resemblance to their closest living relative, the gray wolf (*C. lupus*). While gray wolf subspecies grossly resemble one another, it is typically easy to distinguish a domestic dog from a gray wolf. Domestic dogs generally have smaller heads than gray wolves, most have the ability to or have full-time lowered ears, much smaller vibrissae, smaller teeth and reduced “snouts”. Unlike horses and cats, though, dogs have remarkable variation in not only pelage pattern & coloration on the face but they also have enormous variation in size and shape of the skull, resulting in over 300 recognized breeds today (see Boxes 1 & 2).

Box 2 with Figure 2 -- Examples of the more than 340 recognized dog breeds, demonstrating the range in variation of domestic dogs. A.) Pug, with characteristic brachycephalic (shortened) head and face; B.) Boxer/Bulldog mix displaying brachycephaly; C.) Coonhound, showing dolichocephalic (lengthened) head and face and large ears that lay flat; D.) Pit Bull mix showing dolichocephalic head and face with erect ears and a uniform pelage; E.) Husky, showing erect ears and two “eye dots” above the eyes (red arrow); F.) Mixed breed dog showing “eye dots” above the eyes (red arrow); G.) Chihuahua mix, showing a tiny head and face, large eyes, erect ears, and little fur on the face; H.) Irish terrier, showing a large volume of facial fur.

Unlike domestic cats, domestic dog faces and skulls vary both behaviorally and anatomically from their closest living relative, the gray wolf. The range in variation in domestic dog craniofacial regions is greater than the variation seen in among all other canid species (*e.g.*, Clutton-Brock, 1995). Morphology of dog skulls and faces ranges from brachycephalic (or shortened), as shown here in the pug and the boxer-bulldog mix (A & B) to dolichocephalic (or lengthened), as shown here in the husky and the coonhound (C & E). Unlike gray wolves, most domestic dog breeds have ears that lie flat against the head, with notable exceptions, as shown in A, B, C, F, & H. Additionally, domestic dog breeds display a broad array of pelage patterns and colors, as well as relative volume of fur on the face, from the chihuahua-mix in G with little facial fur to the Irish terrier mix with a high volume of fur in H. Some dog breeds, such as the husky shown here, have colored dots above the medial area of the eye (red arrows). This is also the region where the levator anguli oculi medialis muscle is located in many dog breeds (Kaminski *et al.*, 2019), a muscle that does not seem to be present in gray wolves. The presence of this muscle in some dog breeds, along with the color contrasting markings in the medial area of the eye region, match the critical importance of eye gaze in communication between dogs and humans.

Domestic cat breeds can vary from brachycephalic breeds (such as Persian cats) to relatively dolichocephalic breeds (such as Siamese cats) but these differences do not approach those seen in domestic dogs. Most cat breeds have ears that are erect (with some notable exceptions), like the African wild cat.

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Dogs recognize facial expressions both in other dogs and in humans (Albuquerque *et al.*, 2016), and humans are conditionally adept at reading dogs' facial expressions (Amici *et al.*, 2019). This near-mutual ability is not replicated in our relationships with domestic horses and domestic cats. Humans are, in fact, better at reading dog facial expressions than we are at reading facial expressions in our closest living relative, the chimpanzee (Amici *et al.*, 2019). The bond between humans and dogs is one of the defining characteristics of modern humans. Dogs also engage in mutual gaze with humans to the exclusion of any other species. During this mutual gaze, oxytocin is released in both species and strengthens the care-giving response that many humans feel toward dogs (*e.g.*, Nagasawa *et al.*, 2015). It has even been hypothesized that during the process of domestication, dogs “hijacked” human emotions that resulted in the intense care-giving response that many humans display toward dogs (Kaminski *et al.*, 2019).

During the domestication process, humans may have preferentially associated with gray wolves that displayed affiliative, non-aggressive behaviors that elicited these care-giving responses, resulting in contemporary dog breeds that generally display neotenic facial features relative to gray wolves. The rest is dog history.

Plastic Surgery Informs us Why Dog Faces are Perceived as being Friendlier than Wolf Faces

One of the physical characteristics that strikes the authors is that even at rest, the domesticated animals have kinder, more human-like or human-desired facial features, analogous to some of the features humans desire in themselves (Fig. 1). This is particularly evident looking at the dog vs. the wolf (see Figure 2). The shape of the dog mouth is sometimes upturned, even at rest, almost in a smiling position, whereas the wolf mouth is flatter. In

human facial aesthetics upturned oral commissures (corners of the mouth) are considered more desirable. As people age and facial soft tissues become lax, the corners of their mouth turn down. This oral shape is commonly perceived by others as unpleasant or angry, regardless of the person's actual temperament. Consequently, in the world of aesthetic plastic surgery, this is valued as an undesirable appearance, perceived by others as being unpleasant or grumpy (Larrabee *et al.*, 2003). Amongst other things, aging humans often seek out procedures to correct downturned corners of their mouth (*e.g.*, Botox to the depressor anguli oris muscle, fillers to raise the oral commissure, face lifts, *etc.*) to give them a friendlier, smiling appearance. Perhaps humans selected dogs to have this oral shape because they perceive it as friendly and desirable in a human-like way?

Another example is the shape of the snout or “midface” in profile view. The gray wolf facial shape from upper face (what we would call the “forehead” in humans) to nasal tip is relatively flat (Fig. 1). The dog midface is more human-like, where the snout begins to turn up just distal to the eyes, similar to a human nose. This is nearly pervasive in all of the domesticated dog breeds shown in Figure 2. An analogous difference in facial shape is seen for the domesticated horse in Figure 1 of the current paper. Compared to the wild horse, who has a straight profile from forehead to nose, the domesticated horse has a gentle upward curve to the snout distal to the eyes, more like a human nose. Perhaps humans have selected domesticated animals not just to have a smaller sized snout, but to have one that is more human-shaped. Have humans intentionally or subconsciously domesticated animals to have traits they consider desirable in themselves, making domesticated animals more relatable?

Why do dogs have more facial expressions than cats?

Recent research has demonstrated that domestic horses make 17 individual facial expressions (Wathan *et al.*, 2015) and that domestic cats make 15 facial expressions (Caiero *et al.*, 2017), but humans don't seem to be as good at recognizing these as they are in dogs. Domestic dogs have over 20 facial expressions. For a comparison, chimpanzees have 14 facial expressions (Vick *et al.*, 2007) and humans have 21 facial expressions. While cats have more facial expressions than we might expect, many of these "action units" involve movement of the ears while horse "action units" involve a mix of movements of the ears, nostrils, eyes, and lips. Dogs move the same regions as horses but the range of facial expressions in dogs is broader.

All three of these domestic species have grossly similar arrangements of facial (or mimetic) musculature, with some notable differences. Each species has muscles that attach to the ears, the eye region, the region around the nostrils, and to the lips so differences in the gross musculature offer only partial explanations for why these faces move so differently,

Obviously, living in relatively large social groups is associated with a higher degree of facial mobility (Dobson, 2009a, b) but what are the anatomical underpinnings of this difference? Looking at the microanatomy of mimetic musculature in these species may provide us with some ideas about why the dog face and horse face are more mobile than the cat. Figure 3 shows microanatomical images of the zygomaticus (major) muscle (a muscle common to all three species), histologically stained using hematoxylin and eosin. This muscle is attached to the zygoma and to the soft tissue around the corner of the mouth and this muscle serves to pull back the corners of the mouth. In humans, it helps generate a laugh by pulling the corners of the mouth up and back and in other species, it generates the same movement. Paraffin embedded Zygomaticus mammalian muscles were sectioned at 8um, mounted and

stained using Hematoxylin and Eosin histological staining methods to distinguish cross-sectional areas of connective tissue and musculature. Cut tissue sections were de-paraffinized and rehydrated during sample preparation, followed by regressive H&E staining techniques with the addition of a bluing agent. 2X and 4X images were obtained from each sample and analyzed using light-microscopy.

Box 3 with Figures 3 & 4 Figure 3 shows microanatomical images of zygomaticus major muscles stained with hematoxylin & eosin from (upper left) domestic horse, (upper right) domestic cat, (lower left) gray wolf, and (lower right) domestic dog. The horse sample is so large that a 4X image was necessary in order to show where the muscle is located. Scale bars are each 1mm and each image was photographed at 2X except for the horse inset.

Abbreviations: “CT” – connective tissue; “G” – sebaceous gland; “HS”—hair shaft; “M” – mimetic muscle fibers; “N” – nerve; “SMAS” – superficial musculoaponeurotic system; “VS” – vibrissa shaft. **Figure 4** shows the same region but from a human. The human connective tissue layer (the “SMAS”) is so large that this specimen was photographed at 1X; scale bar represents 1mm.

We know that the unusually high mobility of the human face is due to more than the mimetic musculature itself (Burrows *et al.*, 2016). The superficial musculoaponeurotic system, or SMAS, is a loose fibrous connective tissue layer investing many of the muscles of facial expression and an example is shown in Figure 4. Similar to the way a tendon translates muscle contraction into bone movement, SMAS connects facial muscles both to each other and to dermis to produce facial movement (Larrabee *et al.*, 2003; Mendelson & Jacobson, 2008; Mendelson & Wong, 2012). This allows humans to have an enormous combination of facial expressions of varying and graded amplitude.

This SMAS layer is found in humans (see Fig. 4) over the parotid, buccal, and zygomatic regions of the face, but not in the oral or nasal regions, and this system is considered to be the suspensory mechanism for the soft tissue of the face. (Larrabee *et al.*, 2003). Previous studies have shown that chimpanzees have a reduced but present SMAS while prosimians (nocturnal species that are evolutionarily more distant from humans) did not have this layer, leading to the hypothesis that the SMAS is part of the system responsible for high mobility of the human and chimpanzee face. We argue that the SMAS serves to soften and create smoother facial movements, *i.e.* the graded facial expressions characteristic of humans and, to some extent, chimpanzees.

The domestic cat sample lacks any sign of a discrete connective tissue, “SMAS” layer. Instead, mimetic muscle fibers (the zygomaticus major muscle) fills the section from the epidermis. A large vibrissa shaft is also visible in this section, which reflects the robust and numerous vibrissae that domestic cats have throughout the region of the upper lip. The lack of

a connective tissue, “SMAS-like” layer in the domestic cat, coupled with the presence of dense and large vibrissae may contribute to reduced mobility of the face in this region.

The domestic horse has greater separation between the epidermis of the face and the mimetic muscle layer and this space includes robust connective tissue, but the gap is partially filled with numerous glands and hair follicles. Mobility of the horse face is greater than the cat face (see EquiFACS and CatFACS) and part of this greater mobility may be due to the presence of a connective tissue, “SMAS-like” layer in the horse. See Figure 4 of a human SMAS for comparison.

The gray wolf and domestic dog show relatively thick connective tissue area between the mimetic muscle layer and the epidermis ,and this gap includes relatively few glands and hair follicles. While we do not currently have quantitative data on thickness of this connective tissue layer, these images show that a connective tissue, “SMAS-like” layer is evident in both canids and appears to be roughly the same size. Is it possible that this “potential SMAS layer” is partially responsible for the greater number of facial expressions in domestic dogs (see DogFACS)?

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Box 3 shows that domestic cats have no appreciable connective tissue in this area where we see the SMAS in humans and some other primates while both the domestic dog and gray wolf have a robust layer of connective tissue in the “SMAS area”. It may be this connective tissue layer that accounts for the greater mobility that we see in the dog face relative to both the cat and horse. Given that the gray wolf sample in Figure 3 also has a robust connective tissue layer, is it possible that such a “SMAS-like layer” was already present in the now-extinct

gray wolf populations that gave rise to the first domestic dogs? Without the benefit of a “WolfFACS” to compare with DogFACS, we can’t say how many facial expressions gray wolves have but if these microanatomical images are any clue, we may find similarities between facial expressions in gray wolves and domestic dogs.

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