Domesticated species: It takes one to know one

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Darwin was fascinated by both the process and outcome of our own species' efforts toward the domestication of the plethora of others that became so central to our unparalleled success (1). In fact, he documented many of the various traits and behaviors that we have so purposefully selected. He was clearly enamored by the decreased aggression, increased gregariousness, reduced tooth size, shortened muzzles, smaller brain size, curly tails, floppy ears, increased reproductive success (fertility), and relaxation of the estrus cycle that seemed to accompany such docility. More recent investigations have revealed that domesticated species also possess modified adrenal gland function, novel neurotransmitter levels, and a prolonged juvenile learning period (reviewed in refs. 2 and 3). In PNAS, Kaminski et al. (4) report that an enhancement of the muscles of facial expression can now be added to this list, at least for the domesticated dog. They found that domesticated dogs possess musculature around the eyes that allows them to raise their inner eyebrows, creating an expression that, in humans, is associated with sadness (i.e., "puppy dog eyes"). Equally important is the absence of this trait in wolves, the ancestral species that served as their predomestication ancestor at least 15,000 y ago (5). The evolution of increased facial expressiveness surely has contributed to the canine success of securing their designation as our "best friend."

In terms of the process of domesticating species, it seems that we first honed our skills much closer to home, with ourselves (6). The idea that humans underwent a process of self-domestication has been entertained as a major evolutionary force since Darwin's time. However, Darwin was careful to differentiate the human condition from that of domesticated plants and animals since humans were never subject to controlled breeding by another species (7). Nevertheless, humans and our domesticated animals have a curious collection of traits in common, and it appears that some may well be the result of humans selecting for traits with which they are most familiar (i.e., human-specific traits) (4). We appear to have mirrored ourselves as we reproductively fashioned other mammals for service to our needs. Indeed, it has been proposed that the ultimate form of human expression, language, is also the product of sustained self-domestication (8). Throughout our evolution, there has almost certainly been an intense selection to enhance expressiveness, which, in some form, is likely to have been the ultimate precursor of speech and language. As is well known, the capacity of humans to communicate using facial expressions is unrivaled. Moreover, even the most delicate and subtle glance or passing grimace can elicit strong emotions and actions in others (9, 10). Given the importance of communicating with facial expressions, it is unsurprising that, in the process of domestication, humans imposed intense selection on their canid companions for characteristics that we value in our interactions with one another (4). However, to what does the human capacity of expressiveness, so powerful as to almost effortlessly alter the facial anatomy of the dog (4), owe its origins? Have we almost unknowingly guided our own evolution as much as that of the dog?

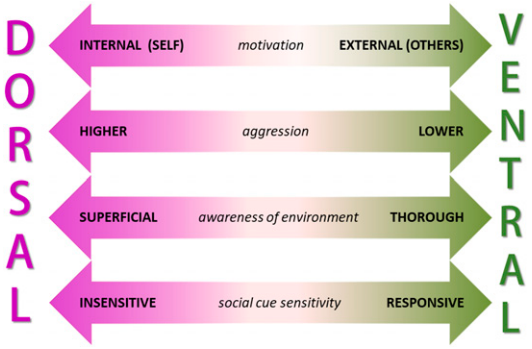

Fig. 1. Differential activity of dorsal versus ventral striatum influences personality types (reviewed in ref. 16).

Critical behavioral characteristics of domestication common to both humans and dogs include

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decreased aggression, increased tolerance and prosociality, cooperation, and an eagerness to please. Such prosociality requires exquisite sensitivity to the cues that comprise all forms of our communication with others. Humans have an exuberant and unparalleled desire to connect with their companions and a remarkable level of altruism that extends to kin, as predicted by sociobiology, and also to nonkin, an odd trait that even crosses species boundaries. This exuberance not only facilitated the domestication of species like dogs and cats but has been extended to heroic altruistic acts to the benefit of potential or even actual predators (e.g., humans will go to great lengths and even risk their lives to save a shark or alligator in distress). While self-domestication is evident in modern humans, its foundations must have been laid much earlier in our evolutionary history, and likely either predated or coincided with the emergence of our most distinctive physical trait—upright walking. That bipedality and reduction of canine size (the "social tooth") appeared simultaneously in the fossil record is surely no accident (11–13). Virtual elimination of the otherwise universal primate social tooth would have required changes within the brain that favored the behaviors associated with domestication, something that we term "personality style." While Phineas Gage provided important information about the seat of personality being in the prefrontal cortex (14), the behaviors that comprise personality styles are not dependent on the expanded neocortex that is the hallmark of modern humans. Personality style, on a basic level, is governed by activity in the striatum (15–18), an ancient structure that was present in early jawless fishes (>500 million years ago) and is involved in both motor control and the reward system. The connection of motor function with personality style was central to establishing alternative ecological niches, and would have relied on variation among individuals as to which cues activate the reward system. Even bluegills exhibit variation in elements of personality style, including habitat preference (littoral regions vs. open water), which coincides with other characteristics such as boldness, activity level, learning ability, and diet (19). It is precisely this type of variation in behavioral characteristics that reinforces habitat preferences, and, in turn, may lead to speciation events.

The striatum has come to play a significant role in the regulation of social behaviors, particularly behaviors that are associated with social reward. Within the striatum, activity of the dorsal versus the ventral striatum corresponds to opposite ends of a continuum of personality styles (Fig. 1) (16, 18, 20–24). The dorsal striatum regulates internally driven, goal-directed behavior. The ventral striatum, in contrast, provides a greater sensitivity to social and environmental cues, and is involved in a system that regulates emotions. The ventral striatum also mediates social conformity in humans (25–28). The motivation for such ventral striatal activity stems from our desire to obtain social approval and to conform with the group (29). It should not go unnoticed that all of these features of the ventral striatum are those that we have clearly chosen to become fixated in the genomes of the common canine. Puppy dog eyes are clearly "designed" to elicit sympathetic acceptance—what can be more true of the typical dog than an intense "other-directed" need to please his human "owner"?

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The incentive component of social interaction is mediated through the brain's (mesolimbic dopaminergic) reward circuit, which, as mentioned earlier, includes major components of the striatum. The hormone oxytocin (sometimes colloquially referred to as "the love hormone") is released when you hug someone or hold someone's hand, and even during eye contact between humans and domesticated dogs (30, 31). It is oxytocin that mediates the rewarding aspects of these interactions by its positive effect on dopamine, the neurotransmitter that is the literal "currency" of the reward pathway (32). We, in our own process of self-domestication, have ultimately recruited prosocial, cooperative, altruistic, and empathetic behaviors to this pathway. Interestingly, the neurochemical signature of the human striatum reflects these changes and is dominated by elevated dopamine (33). While we don't yet know if canids, wild or domestic, possess a striatal neurochemistry similar to our own, it seems likely, given that the traits critical to our own species are now also critical to theirs. The seemingly unquenchable desire of domestic dogs to please their human counterparts (i.e., conform) suggests that they, like humans, have fashioned their own ventral-dominated striatum (Fig. 1).

In terms of base personality styles, wolves possess a certain predisposition to the domestication process (34). Wolves are cooperative, live in large packs, have complex social behavior, rely substantially on male parenting, and are socially monogamous (35). In terms of the personality continuum, wolves are already geared toward its ventral pole (Fig. 1), a situation that may be similar to where our own early ancestors would have been 6 to 8 million years ago. Indeed, the evolutionary trajectory that ultimately led to both modern humans and domesticated dogs could be a case of convergent evolution (36–38). Kaminski et al.'s (4) documentation that the muscles of facial expression that facilitate the human–canine bond are present in domesticated dogs, but absent in wolves, should now serve as a pivotal clue to our own evolutionary history. Humans invariably find puppies irresistible, and the dogs' "sad eyes" can lead them to great success as companions. Indeed, for both humans and dogs, the eyes have it.

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