Oxytocin-Gaze Positive Loop and the Coevolution of Human-Dog Bonds

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The dilution hypothesis provides an alternative framework with which to explain observations of the apparent recalcitrance of DOC and lends a physiological meaning to the operationally defined "semi-labile" and "semi-refractory" fractions (16, 17). We hypothesize that under the dilution hypothesis, very heterogeneous mixtures of labile compounds appear semirefractory, whereas increasingly less diverse DOM assemblages containing larger concentrations of some substrates will present higher microbial growth and DOC turnover rates, resulting in increasing degrees of apparent lability. The microbial generation of apparently recalcitrant material (18) from labile substrates in a process recently dubbed the "microbial carbon pump" (19) can also be explained with the dilution hypothesis. Microbial utilization of abundant, labile compounds results in hundreds of different metabolites (20), which are subsequently consumed down to the lowest utilizable concentration. This mechanism explains observations of relatively concentrated, labile materials being transformed into apparently recalcitrant matter through microbial consumption (18) but does not necessarily imply the formation of structurally recalcitrant molecules. Indeed, "recalcitrant" DOC is not defined structurally, but operationally, as the DOC pool remaining after long experimental incubations or as the fraction transported in an apparently conservative manner with the ocean circulation (1). Thus, the dilution hypothesis severely limits the feasibility of geoengineering efforts to enhance carbon storage in the deep ocean (21) by using the microbial carbon pump.

FT-ICR-MS characterization of DOC from different oceans (13, 14, 22, 23) and also from this study (fig. S5) shows no indication of prevalent, intrinsically recalcitrant compounds accumulating in substantial amounts. Conversely, FT-ICR-MS data show that oceanic DOC is a complex mixture of minute quantities of thousands of organic molecules, which is in good agreement with the dilution hypothesis. Mean radiocarbon ages of deep oceanic DOC in the range of 4000 to 6000 years have been considered as evidence for its recalcitrant nature (24, 25). However, these are average ages of a pool containing a mixture of very old molecules >12,000 years old but also featuring a large proportion of contemporary materials (26). Moreover, elevated radiocarbon ages only demonstrate that these old molecules are not being newly produced at any appreciable rate—because that would lower their isotopic age—but does not necessarily imply that they are structurally recalcitrant. Furthermore, it is unlikely that natural organic molecules can accumulate in the ocean in substantial concentrations and remain recalcitrant or be preserved for millennia when degradation pathways for novel synthetic pollutants evolve soon after these compounds are released in nature (27).

Although there might be a truly recalcitrant component in deep oceanic DOC, our results clearly show that the concentration of individual labile molecules is a major factor limiting the utilization of a substantial fraction of deep oceanic DOC. These results provide, therefore, a robust and parsimonious explanation for the long-term preservation of labile DOC into one of the largest reservoirs of organic carbon on Earth, opening a new avenue in our understanding of the global carbon cycle.

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SOCIAL EVOLUTION

Oxytocin-gaze positive loop and the coevolution of human-dog bonds

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Human-like modes of communication, including mutual gaze, in dogs may have been acquired during domestication with humans. We show that gazing behavior from dogs, but not wolves, increased urinary oxytocin concentrations in owners, which consequently facilitated owners' affiliation and increased oxytocin concentration in dogs. Further, nasally administered oxytocin increased gazing behavior in dogs, which in turn increased urinary oxytocin concentrations in owners. These findings support the existence of an interspecies oxytocin-mediated positive loop facilitated and modulated by gazing, which may have supported the coevolution of human-dog bonding by engaging common modes of communicating social attachment.

Dogs are more skillful than wolves and chimpanzees, the closest respective relatives of dogs and humans, at using human social communicative behaviors (1). More specifically, dogs are able to use mutual gaze as a communication tool in the context of needs of affiliative help from others (2). Convergent evolution between humans and dogs may have led to the acquisition of human-like communication modes in dogs, possibly as a byproduct of temperament changes, such as reduced fear and aggression (1). This idea yields interesting implications that dogs were domesticated by coopting social cognitive systems in humans that

are involved in social attachment. The development of human-unique social cognitive modes may depend on specific temperament and social affiliation changes and may have consequently evolved differently from those of chimpanzees and bonobos (3). Thus, although humans and dogs exist on different branches of the evolutionary tree, both may have independently acquired tolerance of one another because of alterations in neural systems that mediate affiliation (1). These alterations may be related to paedomorphic characteristics in dogs, which enabled them to retain a degree of social flexibility and tolerance similar to that of humans (4, 5); therefore, it is plausible that a specific affiliative relationship developed between humans and dogs despite interspecies differences. This common social relationship change may have enabled cohabitation between humans and dogs and the eventual development of human-like modes of social communication in dogs.

Gaze plays an important role in human communication. Gaze not only facilitates the understanding of another's intention but also the establishment of affiliative relationships with others. In humans, "mutual gaze" is the most fundamental manifestation of social attachment between a mother and infant (6), and maternal oxytocin is positively associated with the duration of mother-to-infant gaze (7). Oxytocin plays a primary role in regulating social bonding between mother and infants and between sexual partners in monogamous species (8, 9). Moreover, activation of the oxytocin system enhances social reward (10) and inhibits stress-induced activity of the hypothalamic-pituitary-adrenal axis (11). It has therefore been suggested that these functions may facilitate dyadic interaction, such as an oxytocin-mediated positive loop of attachment and maternal behaviors between mother and infant (12, 13): Maternal nurturing activates the oxytocinergic system in the infant, thus enhancing attachment; this attachment then stimulates oxytocinergic activity in the mother, which facilitates further maternal behavior (9). Because the establishment of such an oxytocin-mediated positive loop requires the sharing of social cues and recognition of a particular partner, the study of oxytocin-mediated bonding has been restricted to intraspecies relationships.

The human-dog relationship is exceptional because it is an interspecies form of attachment. Dogs can discriminate individual humans (14, 15). Furthermore, dogs show distinctly different behavior toward caregivers as compared with hand-raised wolves (14), and interaction with dogs confers a social buffering effect to humans. Likewise, dogs also receive more social buffering effects from interacting with humans than from conspecifics (16). Tactile interaction between humans and dogs increases peripheral oxytocin concentrations in both humans and dogs (17, 18).

Further, social interaction initiated by a dog's gaze increases urinary oxytocin in the owner, whereas obstruction of the dog's gaze inhibits this increase (19). These results demonstrate that the acquisition of human-like social communication improves the quality of human-dog affiliative interactions, leading to the establishment of a human-dog bond that is similar to a mother-infant relationship. We hypothesized that an oxytocin-mediated positive loop, which originated in the intraspecies exchange of social affiliation cues, acts on both humans and dogs, is coevolved in humans and dogs, and facilitates human-dog bonding. However, it is not known whether an oxytocin-mediated positive loop exists between humans and dogs as has been postulated between mother and infants, and whether this positive loop emerged during domestication.

We tested the hypothesis that an oxytocin-mediated positive loop exists between humans and dogs that is mediated by gaze. First, we examined whether a dog's gazing behavior affected urinary oxytocin concentrations in dogs and owners during a 30-min interaction. We also conducted the same experiment using hand-raised wolves, in order to determine whether this positive loop has been acquired by coevolution with humans. Second, we determined whether manipulating oxytocin in dogs through intranasal administration would enhance their gazing behavior toward their owners and whether this gazing behavior affected oxytocin concentrations in owners.

In experiment 1, urine was collected from the dogs and owners right before and 30 min after the interaction, and the duration of the following behaviors was measured during the interaction: "dog's gaze at owner (dog-to-owner gaze)," "owner's talking to dog (dog-talking)," and "owner's touching of dog (dog-touching)." Dog owners were assigned to one of two groups: long gaze or short gaze (fig. S1). Wolves were tested with the same procedure and were compared with the two dog groups. Dogs in the long-gaze group gazed most at their owners among the three groups. In contrast, wolves rarely showed mutual gazing to their owners (Fig. 1A and fig. S2). After a 30-min interaction, only owners in the long-gaze group showed a significant increase in urinary oxytocin concentrations and the highest change ratio of oxytocin (Fig. 1, B and C). The oxytocin change ratio in owners correlated significantly with that of dogs, the duration of dog-to-owner gaze, and dog-touching. Moreover, the duration of the dog-to-owner gaze correlated with dog-talking and dog-touching (table S2A); however, through multiple linear regression analysis, we found that only the duration of dog-to-owner gaze significantly explained the oxytocin change ratio in owners. The duration of dog-touching showed a trend toward explaining oxytocin concentrations in owners (Table 1A). Similarly, a significantly higher oxytocin change ratio was observed in the dogs of the long-gaze group than in those of the short-gaze group (Fig. 1, D and E). The duration of dog-to-owner gaze also significantly explained the oxytocin change ratio in dogs, and the duration of dog-touching showed a trend toward explaining oxytocin concentrations in dogs by multiple linear regression analysis (Table 1A). In wolves, in contrast, the duration of wolf-to-owner gaze did
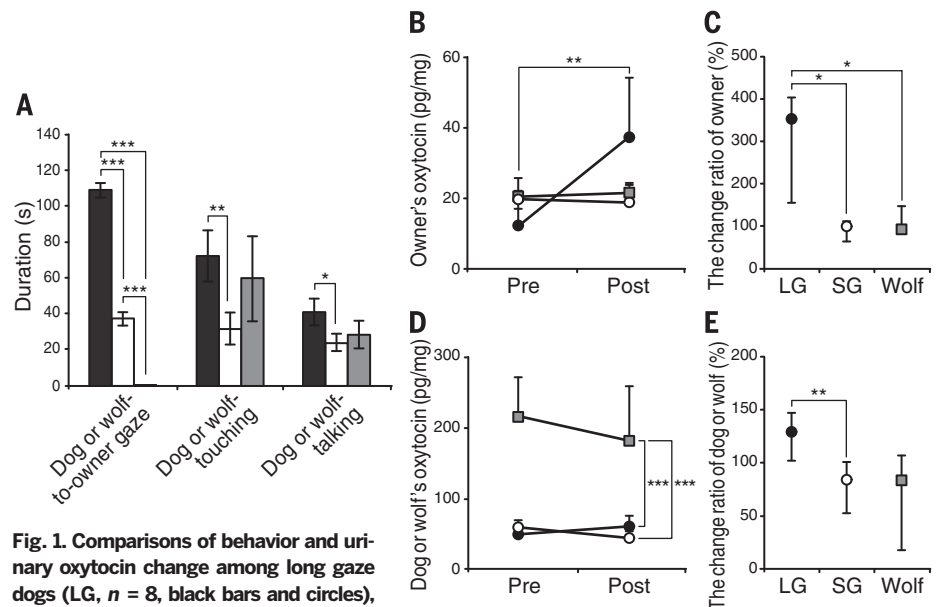

Fig. 1. Comparisons of behavior and urinary oxytocin change among long gaze dogs (LG, n = 8, black bars and circles), short gaze dogs (SG, n = 22, white bars and circles), and wolves (wolf, n = 11, gray bars and square). (**A**) Behavior during the first 5-min interaction. (**B**) and (**D**) Changes of urinary oxytocin concentrations after a 30-min interaction. Urinary oxytocin concentrations in owners (B) and dogs or wolves (D) collected before and after a 30-min interaction are shown. (**C**) and (**E**) Comparisons of the change ratio of urinary oxytocin among LG, SG, and wolf for owners (C) and dogs or wolves (E). The results of (A), (B), and (D) are expressed as mean ± SE. (C) and (E) reflect median ± quartile. ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

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not correlate with the oxytocin change ratio in either owners or wolves, and wolf-to-owner gaze did not explain the oxytocin change ratio in owners and wolves (tables S2B and S3). These results suggest that wolves do not use mutual gaze as a form of social communication with humans, which might be expected because wolves tend to use eye contact as a threat among conspecifics (20) and avoid human eye contact (21). Thus, dog-to-owner gaze as a form of social communications probably evolved during domestication and triggers oxytocin release in the owner, facilitating mutual interaction and affiliative communication and consequently activation of oxytocin systems in both humans and dogs in a positive loop.

In experiment 2, we evaluated the direct evidence of whether oxytocin administration enhanced dog gazing behavior and the subsequent increase in urinary oxytocin concentration in owners. This experiment involved 27 volunteers and their dogs, and participants unfamiliar to the dogs. A solution containing oxytocin or saline was administered to the dog and the dog then entered the experimental room, where the owner and two unfamiliar people were seated (fig. S4). Human behavior toward dogs was restricted to prevent the influence of extraneous stimuli on dog behavior and/or urinary oxytocin concentration. They were forbidden to talk to each other or to

touch the dog voluntarily. Urine samples from the owner and the dog were collected before and after the interaction and were later compared. The total amount of time that the dog gazed at, touched, and was close to the owner and the unfamiliar participants was also measured.

Oxytocin administration to dogs significantly increased the duration that the dog gazed at the owner in female dogs but not male dogs (Fig. 2A). Further, urinary oxytocin concentration significantly increased in the owners of female dogs that received oxytocin versus saline, even though oxytocin was not administered to the owners (Fig. 2D). No significant effect of oxytocin administration was observed in the other measured dog behaviors (Fig. 2, B and C). Furthermore, multiple linear regression analysis revealed that the

duration of gazing behavior significantly explained the oxytocin change ratio in owners (Table 1B). Thus, oxytocin administration enhances the gazing behavior of female dogs, which stimulates oxytocin secretion in their owners. Conversely, when interaction from humans was limited, no significant difference in urinary oxytocin concentrations in dogs was observed after the interaction in either the oxytocin or the saline conditions, and no significant oxytocin change ratio was found in dogs (Fig. 2, F and G). These results thus suggest that, although oxytocin administration may enhance dog gazing behavior and lead to an oxytocin increase in owners, limited owner-to-dog interaction may prevent the increased oxytocin secretion in dogs by breaking the oxytocin-mediated positive loop.

Table 1. Results of multiple linear regression analysis of oxytocin change ratio and behavioral variables in owners and dogs. *$P < 0.05$; †$P < 0.1$; R, multiple correlation coefficient; **, $P < 0.01$.

(A) Experiment 1

	Oxytocin change ratio	
	Owners	Dogs
Owner talking to dog	−0.107	−0.264
Owner touching dog	0.321†	0.335†
Dog-to-owner gaze	0.458*	0.388*
R	0.619	0.575
Adjusted R^2	0.306	0.247
P	0.008	0.020

(B) Experiment 2

	Oxytocin change ratio	
	Owners	Dogs
Dog's sex	0.090	0.138
Oxytocin administration	0.202	0.234
Dog-to-owner gaze	0.458**	0.030
Dog touching owner	−0.040	−0.054
Proximity to owner	0.048	−0.023
R	0.574	0.275
Adjusted R^2	0.248	−0.046
P	0.005	0.686

Sex: Female = 1, male = 0; oxytocin administration: oxytocin = 1, saline = 0.
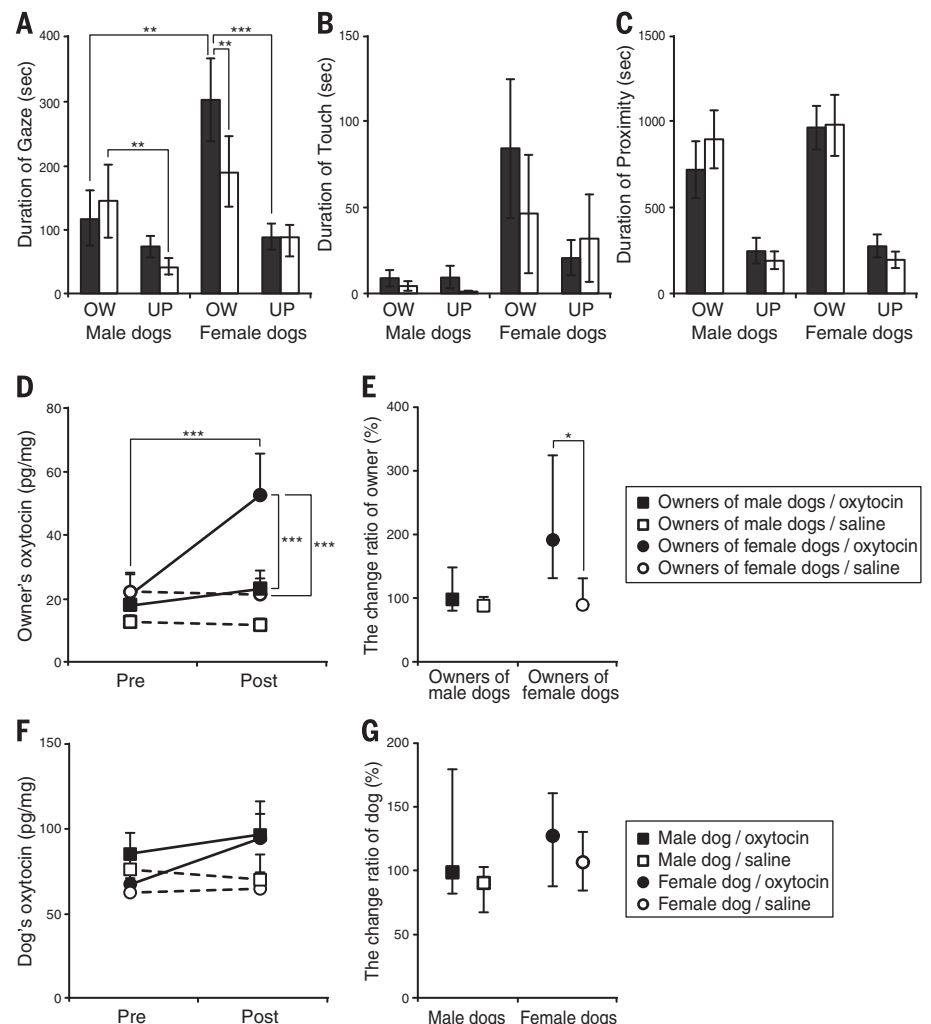

Fig. 2. Comparisons of behavior and urinary oxytocin between oxytocin and saline treatment conditions. (A) to (C) The effects of oxytocin administration on dog behaviors. Panels show the mean duration of dogs' gaze at participants (**A**), touching participants (**B**), and time spent in the proximity of less than 1 m from each participant (**C**). Black and white bars indicate, respectively, oxytocin- and saline treatment conditions. OW, owner; UP, unfamiliar person. (D) to (G) Change in urinary oxytocin concentrations after a 30-min interaction after oxytocin or saline administration. Urinary oxytocin concentrations of owners (**D**) and dogs (**F**) before and after a 30-min interaction are shown for oxytocin and saline groups. The change ratio of urinary oxytocin in owners (**E**) and dogs (**G**) is compared between male and female dogs. ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$. The results of (A) to (D) and (F) are expressed as mean ± SE. (E) and (G) reflect median ± quartile.

Interestingly, oxytocin administration only increased mutual gaze duration in female dogs, whereas sex differences were not observed in experiment 1, which did not include unfamiliar individuals. Sex differences in the effects of intranasal oxytocin have been reported in humans as well (22), and it is possible that females are more sensitive to the affiliative effects of oxytocin or that exogenous oxytocin may also be activating the vasopressin receptor system preferentially in males. Oxytocin and the structurally related vasopressin affect social bonding and aggression in sexually dimorphic manners in monogamous voles (8, 9), and oxytocin possibly increases aggression (23, 24). Therefore, the results of experiment 2 may indicate that male dogs were attending to both their owners and to unfamiliar people as a form of vigilance. The current study, despite its small sample size, implies a complicated role for oxytocin in social roles and contexts in dogs.

In human infants, mutual gaze represents healthy attachment behavior (25). Human functional magnetic resonance imaging studies show that the presentation of human and canine family members' faces activated the anterior cingulate cortex, a region strongly acted upon by oxytocin systems (26). Urinary oxytocin variation in dog owners is highly correlated with the frequency of behavioral exchanges initiated by the dogs' gaze (19). These results suggest that humans may feel affection for their companion dogs similar to that felt toward human family members and that dog-associated visual stimuli, such as eye-gaze contact, from their dogs activate oxytocin systems. Thus, during dog domestication, neural systems implementing gaze communications evolved that activate the humans' oxytocin attachment system, as did gaze-mediated oxytocin release, resulting in an interspecies oxytocin-mediated positive loop to facilitate human-dog bonding. This system is not present in the closest living relative of the domesticated dog.

In the present study, urinary oxytocin concentrations in owners and dogs were affected by the dog's gaze and the duration of dog-touching. In contrast, mutual gaze between hand-raised wolves and their owners was not detected, nor was there an increase of urinary oxytocin in either wolves or their owners after a 30-min experimental interaction (experiment 1). Moreover, the nasal administration of oxytocin increased the total amount of time that female dogs gazed at their owners and, in turn, urinary oxytocin concentrations in owners (experiment 2). We examined the association between our results and early-life experience with humans in dogs and wolves in order to test the possibility that our results were due to differences in early-life experience with humans. The results did not indicate a significant association between the animals' early-life experiences with humans and the findings of the current study (see the supplementary methods). Moreover, there were no significant differences between dogs in the long-gaze group and wolves in either the duration of dog/wolf-touching and dog/wolf-talking, suggesting that the shorter gaze of the wolves was not due to an unstable relationship. These re-

sults support the existence of a self-perpetuating oxytocin-mediated positive loop in human-dog relationships that is similar to that of human mother-infant relations. Human-dog interaction by dogs' human-like gazing behavior brought on social rewarding effects due to oxytocin release in both humans and dogs and followed the deepening of mutual relationships, which led to interspecies bonding.

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PLANT ECOLOGY

Anthropogenic environmental changes affect ecosystem stability via biodiversity

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Human-driven environmental changes may simultaneously affect the biodiversity, productivity, and stability of Earth's ecosystems, but there is no consensus on the causal relationships linking these variables. Data from 12 multiyear experiments that manipulate important anthropogenic drivers, including plant diversity, nitrogen, carbon dioxide, fire, herbivory, and water, show that each driver influences ecosystem productivity. However, the stability of ecosystem productivity is only changed by those drivers that alter biodiversity, with a given decrease in plant species numbers leading to a quantitatively similar decrease in ecosystem stability regardless of which driver caused the biodiversity loss. These results suggest that changes in biodiversity caused by drivers of environmental change may be a major factor determining how global environmental changes affect ecosystem stability.

Human domination of Earth's ecosystems, especially conversion of about half of the Earth's ice-free terrestrial ecosystems into cropland and pasture, is simplifying ecosystems via the local loss of biodiversity (1, 2). Other major global anthropogenic changes include nutrient eutrophication, fire suppression

and elevated fire frequencies, predator decimation, climate warming, and drought, which likely affect many aspects of ecosystem functioning, especially ecosystem productivity, stability, and biodiversity (1, 3–7). However, to date there has been little evidence showing whether or how these three ecosystem responses may be mechanistically