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Increase of tear volume in dogs after reunion with owners is mediated by oxytocin

Kaori Murata[1,6], Miho Nagasawa[1,2,6], Tatsushi Onaka[3], Nobuyuki Kanemaki[1,4], Shigeru Nakamura[5], Kazuo Tsubota[5], Kazutaka Mogi[1,2], and Takefumi Kikusui[1,2,*]

In humans, tear volume increases during emotional arousal. To our knowledge, no previous studies have investigated the relationship between emotional arousal and tear volume in animals. We performed the Schirmer tear test (STT) and measured tear volume in dogs before and after reunions with owners and familiar non-owners. Tear volume increased significantly during reunion with the owner, but not with a familiar non-owner. When an oxytocin solution was applied to dogs' eyes, the tear volume also increased, suggesting that oxytocin might mediate tear secretion during owner–dog reunions. Finally, human participants rated their impressions on photos of dogs with or without artificial tears and they assigned more positive scores to the photos with artificial tears. These results suggest that emotion-elicited tears can facilitate human–dog emotional connections.

Dogs reportedly have human-like social-cognitive skills, which are thought to result from convergent evolution with humans[1]. Eye contact plays a pivotal role in attachment behavior in dogs, with eye contact between dogs and humans eliciting human caregiving behavior[2]. It is also hypothesized that canine tear production during reunions with owners can facilitate human caregiving, a phenomenon which has similarly been reported in human children[3]. Furthermore, dogs have evolved muscles responsible for raising the inner eyebrows, which trigger nurturing behavior in humans[4]. A dog's gaze initiates interactions with its owner, and stimulates secretion of oxytocin, a key hormone involved in bond formation, in owners[2].

Humans often exhibit increased lacrimation, which appears as tears, in situations involving physical pain. Interestingly, humans also have tears that are secreted in response to emotional arousal, both in positive and negative situations[3]. It can be said that tears also play a role in nonverbal communication, for example when humans are in a negative state, such as hunger, pain, or discomfort, or in a positive state, such as during reunions with family or friends, in which tears serve as a trigger eliciting human interaction[3].

When dogs reunite with their owners, they exhibit highly affiliative behavior, including gazing at their owners, wagging their tails, jumping up, and licking their owner's faces (Video S1 in Supplemental information, published with this article online). Physiologically, oxytocin concentrations increase in dogs during reunion with humans[5].

In this study, we hypothesized that dogs secrete tears during reunions with their owners, that tear secretion is mediated by oxytocin, and that tears in dogs' eyes could facilitate human caregiving behavior. In the first experiment, the dogs' tear volumes were measured by STT in their normal home environment with the owner present (baseline), and within the first 5 min of a reunion with the owner following 5 to 7 hours of separation ($n = 18$). A mixed model analysis revealed that tear volume significantly increased during the reunions ($p < 0.01$, $F(1,16) = 8.54$, linear mixed model) (Figure 1A). Secondly, we compared tear volumes before and after reunions with owners and familiar non-owners. Following separation from the owner in the dogs' day care centers, dogs secreted larger tear volumes during reunions with their owners than with familiar non-owners, and tear volume during reunion with the owner was significantly greater than the baseline tear volume ($p < 0.05$, $F[1,54] = 4.35$, linear mixed model) (Figure 1B). To assess the role of oxytocin in tear production in dogs, solutions of oxytocin and a control peptide comprising the same amino acids but re-arranged were applied to the ocular surface and tear volume was measured. Tear volume was significantly increased after oxytocin administration, but not after the control peptide solution ($p < 0.05$, $F(1,60) = 6.57$, linear mixed model) (Figure 1C).

It was hypothesized that the tears in dogs' eyes during reunion facilitate human caregiving to dogs, as in the case of interactions with human children[3]. To test this hypothesis, we had human participants rate their impression of photos of dogs' faces with or without artificial tears in terms of how much they wanted to care for them. The dog photos with artificial tears were ranked significantly higher than the normal tearless dog photos ($p < 0.01$, Wilcoxon signed-rank test) (Figure 1D).

Recent studies have focused on the neural mechanisms underlying tear secretion. In mouse models, oxytocin has been shown to stimulate tear secretion by acting on the oxytocin receptors expressed in the lacrimal glands[6]. Another study in mice demonstrated that oxytocin neurons located in the paraventricular hypothalamus send fibers to the superior salivary nucleus and are involved in increasing tear production. Therefore, oxytocin increase related to positive and negative emotional arousal can facilitate tear secretion, acting on both central and peripheral organs[7]. One point to note is that oxytocin administration also acts on vasopressin receptors, so it will be necessary to clarify in the future which receptors were affected by the results of this administration experiment.

The social functions of oxytocin-stimulated tears are currently unclear. In mammals, tears can function as chemosignals; for example, male mouse tears contain the sex pheromone ESP1, which stimulates female sexual behavior and male aggression[8]. Even in humans, tear fluid contains some chemo-signals and tears are used as socio-sexual signals[9]. Sniffing and licking near the eyelid is commonly observed behavior when dogs greet one another, suggesting a possibility that dogs' tears also play a role as a social signal.

In humans, infants use tears to transmit negative feelings to their parents, and in response to that the receivers show caregiving behavior[3]. In this study, we found that a dog's face with artificial tears can also stimulate caring emotions in humans. Even though the tear volume increased after reunion with the owner in this study,

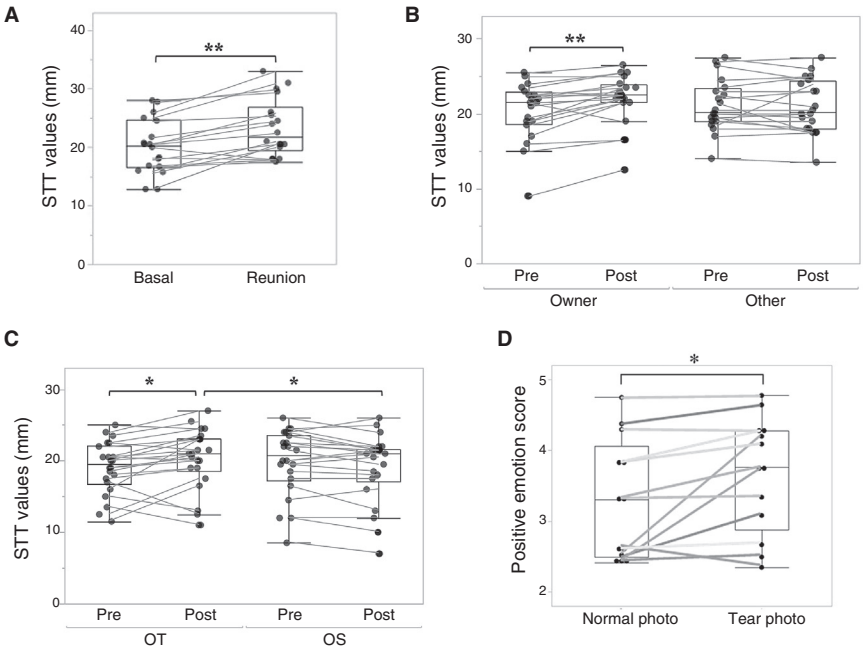

Figure 1. Tear volume increased by reunion with the owner and oxytocin administration.
(A) Tear volume after reunion with the owner. Tear volumes were measured by the Schirmer Tear test (SST), expressed as the length of the wetted part of the test paper (Figure S1B). The baseline was the volume measured when the dogs stayed with their owner at home. Tears during the reunion were measured in dogs that were separated from the owner for more than 5 hours, and within the first 5 min of reunion. (B) Tear volume during the reunion with the owner and with the familiar non-owner. Tear volume was measured in the dog's day-care center. Pre-volume (Pre) was measured before the reunion, and post-volume (Post) was measured during the first 5 min of reunion after separation from the owner for more than 5 hours. (C) Oxytocin (OT) and control peptide (comprising the same amino acids as oxytocin, but with the sequence scrambled; OS) were dissolved in sterile saline (20 IU/120 μL) and dropped onto the ocular surface of both eyes. The STT was conducted 5 min after administration. Of the 22 animals, 11 received OT first, and the remaining 11 received OS first, to counterbalance the order of eye administration. (D) The rating scale of human participants after watching dog face photos (Figure S1C). A pair of photos was prepared for each dog: a picture of the dog with unaltered eyes and one of the dog where sterile saline was applied to the eyes. 10 photos from 5 dogs were randomly presented on the computer screen, and the participants scored on a 5-point scale from positive (want to touch, and give some care) to negative (fearful and avoid) for each photo (Figure S1A). (*$p < 0.05$, **$p < 0.01$).

the social functions of tears in dogs are unclear. Two aspects of dog tears need to be addressed. One is their function as chemo-signals among conspecifics and the other is their ability to elicit caregiving behavior in humans.

In this study, we demonstrated that dogs secrete tears when reuniting with their owner, and our data suggest that this tear secretion is mediated by oxytocin. This is the first report on positive emotion stimulating tear secretion in a non-human animal, and oxytocin functioning in tear secretion. Unlike any other animals, dogs have evolved or have been domesticated through communication with humans and have gained high-level communication abilities with humans using eye contact[2]. Through this process, their tears might play a role in eliciting protective behavior or nurturing behavior from their owners, resulting in the deepening of mutual relationships and further leading to interspecies bonding.

SUPPLEMENTAL INFORMATION

Supplemental information contains one figure, experimental procedures, and one video which can be found with this article online at https://doi.org/10.1016/j.cub.2022.07.031.

A video abstract is available at http://dx.doi.org/10.1016/j.cub.2022.07.031#mmc3.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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[1]School of Veterinary Medicine, Azabu University, 1–17–71 Fuchinobe, Chuou-ku, Sagamihara, Kanagawa 252-5201, Japan. [2]Center for Human and Animal Symbiosis Science, Azabu University, Kanagawa 252-5201, Japan. [3]Division of Brain and Neurophysiology, Department of Physiology, Jichi Medical University, Tochigi 329-0498, Japan. [4]DVMs Animal Medical Center Yokohama, 2-2 Sawatari, Kanagawa-ku, Yokohama, Kanagawa 221-0844, Japan. [5]Department of Ophthalmology, Keio University School of Medicine, Tokyo 160-8582, Japan. [6]These authors contributed equally.
*E-mail: kikusui@azabu-u.ac.jp