



High interindividual and intraindividual variation of oxytocin secretion in estrous mares exposed to stallions, but no significant link to mate preferences

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ABSTRACT

Oxytocin is a hormone that may not only influence reproductive mechanisms in mammals but also their social behavior, including pair bonding. We therefore tested if the concentrations of oxytocin and other hormones reveal mate preferences of 13 mares in estrus. Each mare was first exposed to two stallions (haphazardly selected out of seven) and her behavior recorded. The mare was then returned to her box (i.e., no contact to stallions during that time). Approximately 4.5 hours later, venous blood samples were collected every minute during 30 minutes preceding exposure to one of the two previously used stallions, 6 minutes during exposure, and 30 minutes after exposure back in the mare's box. The procedure was repeated in the consecutive estrus cycle, with the difference that the mare was each exposed to the other of the two stallions during oxytocin measurements. In 20 of the 26 trials, oxytocin concentrations were significantly elevated during exposure to the stallion, without significant associations to cortisol and estradiol concentrations. We found no significant association between oxytocin secretion and preferences in the previous choice situation. While estradiol concentration showed a high repeatability over the two cycles, we found considerable intraindividual differences in oxytocin and cortisol plasma concentration among the two cycles. Partially, the variation in oxytocin concentrations could be linked to the time of ovulation, with lower oxytocin plasma concentrations in mares which ovulated later than expected. In conclusion, when teasing under experimental conditions, we found high interindividual and intraindividual variation among mares in the increase of oxytocin plasma concentrations, depending on the timing of ovulation. However, oxytocin levels seemed to be no predictor of mare preference.

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1. Introduction

Sexual stimulation (so-called teasing) of a mare with a stallion is a way of detecting estrus and hence represents an important tool to determine the ideal time for in hand

breeding or artificial insemination in horses (*Equus caballus*). Teasing is also assumed to provoke an endogenous release of oxytocin in the estrous mare [1–3] hereby enhancing uterine contractions [1,4]. While teasing, the mare is usually exposed to a stallion that is spatially separated from the mare so that he cannot fully interact with her, for example, the two can only interact over a fence, a stall door, or a chute designed specifically for this purpose. The mare's behavioral responses to the

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stallion are then observed to assess her estrus status [5]. Estrous signs include repeatedly approaching the stallion, frequent urination, clitoral winking (rhythmic eversion of the clitoris), deviating the tail away from the perineum, and rotating the body so that the hindquarters are in front of the stallion and standing still with the hind limbs spread apart [5,6].

The nonapeptide oxytocin is a hormone that regulates several reproductive mechanisms in mammals, such as uterine contractions during parturition and milk ejection in the lactation period [7,8]. Oxytocin released within the central nervous system was also shown to play a major role in inducing maternal behavior in various species, including horses [9]. Recent studies in humans show that oxytocin also influences other behavior and behavioral strategies, for example, social recognition [10,11], trust building [12,13], reduction of stress and anxiety [14] as well as pair bonding [15]. In animal experiments, effects of oxytocin on social and affiliative behavior have been well documented (see reviews [16,17]). Oxytocin administration or restriction can result in alterations of preference formation in female prairie voles [18] and also socio-sexual behavior patterns between pair mates and the resulting mate choice between a stranger and a familiar pair mate, as found in marmosets [19].

Besides teasing, also other stimuli such as stallion vocalization, visual contact with a stallion, manual cervical dilation, artificial insemination, and mating have been shown to induce an oxytocin release in the mare [1–3,20]. On the other hand, it becomes evident, that not all mares release oxytocin in response to teasing. Measuring the concentrations of oxytocin in intracavernous sinus blood samples, Madill et al. [1] could demonstrate an oxytocin peak after teasing in only four out of five mares. In the study of Nikolakopoulos et al. [2], only six out of 10 estrous mares displayed a significant oxytocin increase in jugular venous blood samples after teasing. Reasons for this observation are not yet fully understood and have so far not been evaluated in a behavioral or evolutionary perspective. One possibility is that the variation in oxytocin levels reflects individual mate preferences. Sexual selection by female choice could be shown in a wide variety of species (reviewed in [21]). In feral harems, more than 88% of stallion-mare interactions that lead to successful copulation are initiated by the mare [22]. Studies on the interactions between mares and stallions show individual sexual preferences of estrous mares for certain stallions (D. Burger et al, unpublished work, 2016) [23].

Here, we test whether estrous mare oxytocin plasma concentrations during short-term exposure and teasing to stallions can be related to her mate preferences. In this context, the horse can be seen as a suitable experimental model, as this polygamous mammal offers by its size and manageability optimal conditions for repetitive manipulation and sample collection. This in turn allows for direct hormonal analyses, resolving difficulties in obtaining and interpreting plasma oxytocin as its release is pulsatile and therefore needing a frequent and rapid sampling to be accurately determined [8]. We therefore measured oxytocin plasma concentrations before, during, and after teasing mares with two different stallions each. The mare's

reaction toward these stallions was previously recorded in a preference test. In addition, we investigated potential associations between oxytocin blood levels and stallion characteristics such as age, size and weight, or mare characteristics such as ovulation time or plasma estradiol and cortisol concentrations.

2. Material and methods

2.1. Animals and infrastructures

Twenty clinically healthy horses (13 mares and seven stallions) were used in this study. The mares were non-lactating, 8 to 20 years old (mean \pm standard deviation [SD]: 12.6 ± 3.5 years), 1.52 to 1.72 m high (1.60 ± 0.06 m), weighing between 502 and 662 kg (581.2 ± 57.3 kg), and of various breeds (nine Warmblood, two Franches-Montagnes, and two Standardbred). All mares had normal perineal conformation and ovarian activity with variable reproductive histories. The stallions were 4 to 16 years old (10.6 ± 4.6 years), 1.52 to 1.61 m high (1.56 ± 0.03 m), and weighing between 477 and 610 kg (524.6 ± 41.9 kg). All of them were from the Franches-Montagnes breed and had natural service breeding experience with proven fertility.

Experimental infrastructures consisted of one stable with eight boxes each of 12 m², separated by 1.47-m high wooden walls and above a 2.00-m high metal grill, with a window (0.68 \times 0.75 m) toward the corridor, allowing visual, olfactory, and limited physical contact with the mare. Transrectal ultrasonographic examinations were performed with a 5-MHz linear array transducer (Aquila Pro VET, Esaote, Genova, Italy).

2.2. Study design

The experiments were performed during the physiological breeding season from May to August in the Swiss National Stud in Avenches by always the same persons. In a standardized procedure (see Fig. 1), every mare was exposed to two different stallions each (out of the seven stallions). The two stallions had been haphazardly assigned to each mare and the two trials were performed in two consecutive estrus cycles.

Mares entered each trial after having been confirmed to be in estrus using behavioral observation (teasing with a stallion that was not used in later experiments) and transrectal ultrasonography (endometrial edema and pre-ovulatory follicle ≥ 35 mm in diameter). Mares were individually stabled in clean boxes the day before the experiment. Another mare from the herd was stabled in the box beside the experimental mare to minimize eventual stress responses due to the environmental changes. At 7 PM, the experimental mare was treated with 1500 IU human chorionic gonadotropin (hCG) intravenously (Chorulon, Intervet, Boxmeer, Netherlands) to induce ovulation.

2.2.1. Preference test

At 9 AM the following day, the mares' reactions toward two stallions were studied in a preference test. For that reason, before 9 AM, the stallions were led into the experimental stalls. In the mare's first estrus cycle, the stallions'

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