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Testosterone dependent territorial aggression is modulated by cohabitation with a female in male Mongolian gerbils (*Meriones unguiculatus*)

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ABSTRACT

Most mammal studies on the neuroendocrine mechanisms of territorial aggression have demonstrated that testosterone (T) is required for the display of territorial aggression. However, the relationship between T and aggression is more complex and may be modulated by social factor. The aim of this study was to determine the role of T in territorial aggression in the Mongolian gerbil (*Meriones unguiculatus*), and the effect of social factors on the modulation of this behavior. The relationship between T and territorial aggression was analyzed using castration and T replacement in two social contexts: male-male and male-female cohabitation. Plasma T concentrations in males of all groups were quantified by radioimmunoassay (RIA). T concentrations were compared using two-way ANOVA. Only sham-castrated and castrated males with T replacement in male-female cohabitation showed aggression, whereas castrated gerbils in the same condition were not aggressive. This indicates that T is the hormone that maintains territorial aggression, but mating is a modulator stimulus. The modulator effect of mating in territorial aggression was associated with an increase in T, but it seems that other mechanisms are involved in the regulation of this behavior, since castrated males with T replacement in the male-male cohabitation did not exhibit aggression, although they had T concentrations as high as these males that received the same treatment, but that cohabited with a female. These results suggest that T is involved in the mechanisms that regulate territorial aggression in the male Mongolian gerbil, and that the cohabitation with a female modulates this behavior.

1. Introduction

Aggression is displayed by all animals and has a wide range of adaptive functions. Aggressive behavior is a strategy to resolve conflicts and is displayed when individuals of the same species, and even different species, compete for limited resources. Aggression has been classified in different ways according to the social context in which it is displayed (Moyer, 1971), and more recently it was classified as either offensive or defensive (Blanchard and Blanchard, 1988). Territorial aggression is one of the most studied types of aggression, this behavior is displayed when there is competition for resources, *for example*, territory, mates, and or food, all of them present in a sociogeographical area (Scotti et al., 2015; Soma et al., 2015). Physical aggression may be avoided displaying submissive postures or ritualized fighting (Soma et al., 2008; Trainor and Marler, 2010). Aggression is characterized by a set of species-typical behaviors performed in close interaction with the opponent. In rodents, fighting between two males typically includes chasing, boxing, clinch attack and biting (Takahashi and Blanchard, 1982; Trainor and Marler, 2010).

Aggressive behavior has a high cost, and therefore it is tightly regulated by multiple levels of control that integrate information about the physical and social environments (Wingfield and Soma, 2002; Trainor and Marler, 2010). Most endocrine research on territorial aggression has focused on testosterone (T); several studies performed on rodents, have reported that male aggression is reduced by castration, and restored by T replacement (Payne, 1972; Sayler, 1970; Brain and Haug, 1992; Soma et al., 2015; Duque-Wilckens et al., 2019). However, there is evidence that the relationship between T and aggression is more

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complex and may be modulated by social factors such as mating and social structure (Crews and Moore, 1986; Gleason et al., 2009). For example, the presence of an oestrus female increases the T dependent aggression in the rat (Taylor et al., 1984). Males of a variety of mammal species respond to female stimuli by triggering an increase in luteinizing hormone followed by a rise in plasma T (Macrides et al., 1975; Coquelin and Bronson, 1980; Rone et al., 2007). T release occurs in other social contexts such as after an aggressive encounter (Gleason et al., 2009).

As indicated earlier, the relationship between T and aggression has been studied mostly in rats and mice males from different laboratory strains, but more research needs to be done in non-conventional species. Thus, the Mongolian gerbil (*Meriones unguiculatus*) is here used as a study model. This rodent is a monogamous species inhabiting in semi-deserts and steppes in Mongolia. Male gerbils give the same care to pups just like the mother, except for suckling (Marston and Chang, 1965; Elwood, 1975). Previous studies about the function of T in territorial aggression of this rodent have reported inconsistent results: Sayler (1970) indicated that castration after four months of isolation significantly reduced aggression, whereas Christenson et al. (1973) reported that castration increased aggression when the males were gonadectomized after six months of isolation). Another study pointed out that aggression was decreased by castration, while T replacement stimulated aggressive behavior, also using the isolation paradigm (Yahr et al., 1977). In this context, the aim of this study was to determine the role of T in territorial aggression and the effect of social factors such as male-female and male-male cohabitation on the modulation of this behavior in the Mongolian gerbil (*Meriones unguiculatus*).

2. Material and methods

2.1. Animals

Virgin male Mongolian gerbils between 160 and 210 days old were used. These gerbils were obtained from a colony kept at the Facultad de Estudios Superiores Iztacala, UNAM. The colony was maintained under an inverted photoperiod of 12:12 h (light-dark cycle; the onset of light at 1800 h) at an ambient temperature of between 18 °C and 22 °C, and humidity between 40% and 60%. The gerbils were fed pellets with Lab Chow 5001 (Nutrimentos Purina, México) and tap water *ad libitum*. From weaning until the onset of the experiment, two male gerbils were housed in a polycarbonate cage (32 cm × 23 cm × 15 cm) with sawdust bedding.

The relationship between territorial aggression and T was analyzed in two social contexts: male-female and male-male cohabitation. The gerbils were organized into two groups: in the Group 1; 54 males were maintained in male-male cohabitation (27 pairs), and in the Group 2; 27 males cohabited with a female. Nine males of both Group 1 and Group 2 were castrated, another 9 males were submitted to sham procedure, and the remaining 9 underwent castration and T replacement. In the Group 1, a randomly chosen male of each pair received treatment, while the other male remained intact. These treatments were performed 15 days after cohabitation period. Twenty-four hour after the castration or sham castration the males were returned to their respective house-cages. During the cohabitation period sawdust bedding was partially changed to preserve the characteristic gerbil odours. The cohabitation cage was a polycarbonate (63 × 40 × 20 cm). Resident-intruder tests were conducted between 10 and 12 days after the treatments. The 88.8% (n = 26) of the females cohabiting with males became pregnant because they gave birth their pups, unequivocal evidence of mating.

All the experiments were performed in accordance with the ethical guidelines of the National Institutes of Health Guide for the Care and Use of Laboratory Animals (NIH Publication No. 8023) and the ethical guidelines of the Official Mexican Standard that regulates technical specifications for the production, care and use of laboratory animals (Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación, 2001).

2.2. Surgeries and implants

The gerbils were anesthetized with 10 mg/kg of xylazine and 90 mg/kg of ketamine before surgery and placement of T implants. Only sterile surgical instruments were used. Antibenzil was applied to disinfect the scrotum, a small midline incision was made, and the testes were exteriorized. The spermatic vessels were tied with 6.0 silk sutures, and the testes were removed. The incision was then closed with 6.0 silk sutures. In the sham-operated gerbils, the skin of the scrotum was incised, the testes were drawn out and returned, and the incision was closed with sutures only. At 48 h after surgery, the gerbil was returned to the home cage. Implants were made of silastic tube (Silastic Laboratory Tubing, i.d. 1.47, o.d. 1.96 mm) packed with 10 mm of testosterone propionate (Sigma Aldrich, St. Louis, MO, USA); the two ends were sealed with silicone. The T implant was placed under the skin of the back. Acetylsalicylic acid ~100 mg/kg was orally administered as an analgesic for the first 12 h following surgeries.

2.3. Resident-intruder test

Behavioral tests were performed 10 to 12 days after the surgery and T replacement. Two minutes before starting the resident-intruder test, the intact male or female was removed from the home cages of the male-male or male-female cohabitation. After 10 min, a strange male similar in age and weight to opponent was put in the home cage. Attack latency and aggressive and non aggressive behaviors were record. The test ended after 15 min irrespective or whether aggression was displayed. Frequency attack was not recorded since confrontations were stopped when the intruder male was attacked by the resident male to avoid damage to the gerbils. The observations were carried out by one researcher during the dark phase between 11:00 and 15:00. For observation, we used the focal method. Fifty intact sexually inexperienced males were used as intruders, these gerbils remained as two individuals per cage as experimental animals. Some of these gerbils were used twice as intruder, but not on the same day.

2.4. Hormone assay

Immediately after the end of the resident-intruder test, blood samples were obtained from the retro-orbital sinus with heparinized capillaries under light anesthesia (5 mg/kg xylazine and 60 mg/kg ketamine). Each sample was obtained approximately for 1 min. The plasma was separated by centrifugation and stored at −40 °C. T analysis was performed using a radioimmunoassay (RIA). The RIA was performed in duplicate using a Siemens Total Testosterone Kit (Diagnostic Products Corporation, Los Angeles, CA, USA), with ^{125}I testosterone having a sensitivity of 4.0 ng/dl. Inter and intra-assay coefficients of variation were 4.0% and 6.9%, respectively. The T assay was validated, and it demonstrated a correlation between the dilutions of serum from Mongolian gerbils and the standard curve. The recovery rate for T was 88.0% (r = 85.0). The radioactivity was measured with a gamma counter model 1282 Compugamma (LKB-Wallac, Turku, Finland).

2.5. Statistical analysis

Because only sham-castrated males and castrated males with T replacement in cohabitation male-female displayed aggression, we analyzed between-group differences in attack latencies using the Student *t*-test for independent groups.

Peripheral T levels between castrated males, sham-castrated males and castrated males with T replacement in the male-male and male-female cohabitation conditions were compared using two-way ANOVA. As the data did not meet the normality criteria of the Anderson–Darling

Table 1
One hundred percent of males that undergoing castration + T replacement and sham-castration males that cohabited with their mates displayed aggression.

Cohabitation	Treatments	Aggression in resident-intruder test
Male-male	Castration	0.0%
	Castration + T	0.0%
	Sham castration	0.0%
Male-female	Castration	0.0%
	Castration + T	100%
	Sham castration	100%

test ($P < 0.05$) we proceed as follows: data were transformed to log (x + 1) to avoid negative values because several data of T concentrations were < 1. Post hoc comparisons were made using a Tukey test. The Spearman correlations between the attack latencies and T concentrations were performed for the sham castrated and castrated males with T replacement in male-female cohabitation because the males maintained under that condition displayed aggressive behavior.

Statistical analyses were performed using SPSS version 21.0 (IBM SPSS, Armonk, NY).

3. Results

3.1. Behavioral data

The results showed 0.0% of castrated males, 0.0% of castrated +T males and 0.0% of sham-castrated males in the male-male condition displayed aggression in the resident-intruder test. Also, 0.0% of castrated males in male-female cohabitation exhibited aggression. However, 100% of the castrated + T males and sham castrated males that cohabited with a female displayed aggression (Table 1). During aggressive encounters between the Mongolian gerbil males, the first interaction with the intruder was the recognition; the resident male sniffed intruder male for 2 to 3 s, and after the intruder male fled, whereas resident male chases him. Then this male attacks intruder male, who typically responds by either running away or showing a steoreotyped submissive posture.

3.2. Attack latency

Attack latencies of sham-operated males and castrated males with T replacement were not significantly different ($t = 1.08$, $DF = 9$, $P > 0.05$, Cohen's = 0.26, Fig. 1).

3.3. Testosterone concentrations

Peripheral T concentrations between the castrated males, sham-castrated males and castrated males with T replacement in the male-male and male-female cohabitation conditions were significantly different (treatment, $F = 229.82$, $DF = 2/53$, $P < 0.05$; condition $F = 18.55$, $P < 0.05$; interaction $F = 5.12$, $P < 0.05$, $\eta^2 = 0.01$, Fig. 2). Multiple comparisons showed that T levels in the castrated males with T replacement in the two conditions of cohabitation (male-male and male-female) were significantly higher than in the sham-castrated and castrated males ($P < 0.05$) in male-male and male-female cohabitation. The sham-castrated males that cohabited with a female had T concentrations significantly higher than those sham-castrated males that cohabited with a male ($P < 0.05$). T concentrations between castrated males that cohabited with a female or a male were not significantly different. The T levels were not significantly correlated with the attack latencies in the sham-castrated ($r = 0.46$. $P > 0.05$), and castrated males with T replacement ($r = 0.18$, $P > 0.05$), which displayed territorial aggression.

4. Discussion

The sham-castrated and castrated males with T replacement housed in the male-female condition displayed aggression, whereas castrated males under the same condition did not exhibit aggressive behavior, this indicates that gonadal T is the hormone that maintains the territorial aggression in the Mongolian gerbil. These results are according to those obtained by Sayler (1970) and Yahr et al. (1977), in which castration eliminates aggression. However, it contradicts the results reported by Christenson et al. (1973), who mentions that castration increases aggression. This may be due to use different experimental designs, these researches utilized the isolation as aggression paradigm, this condition caused stress, which possibly increased the aggressive behavior by a different pathway as T does (Brain, 1975; Moya-Albiol

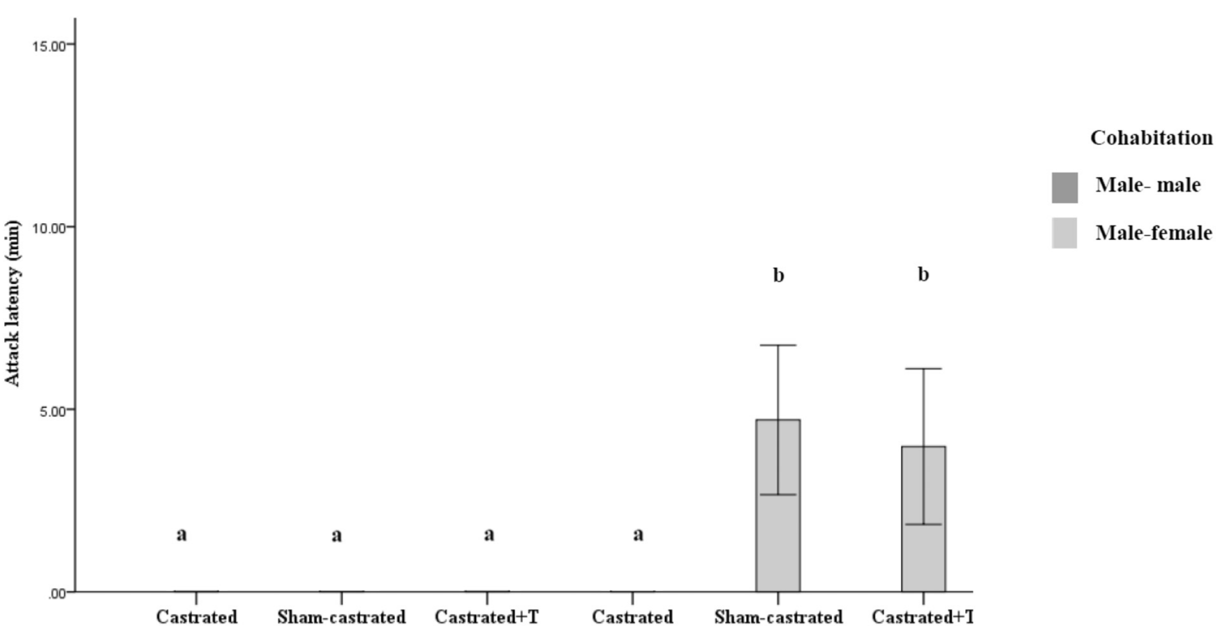

Fig. 1. Only males that cohabitated with a female displayed territorial aggression when T was present. Data are represented in means and SE. The letters indicate significant differences.

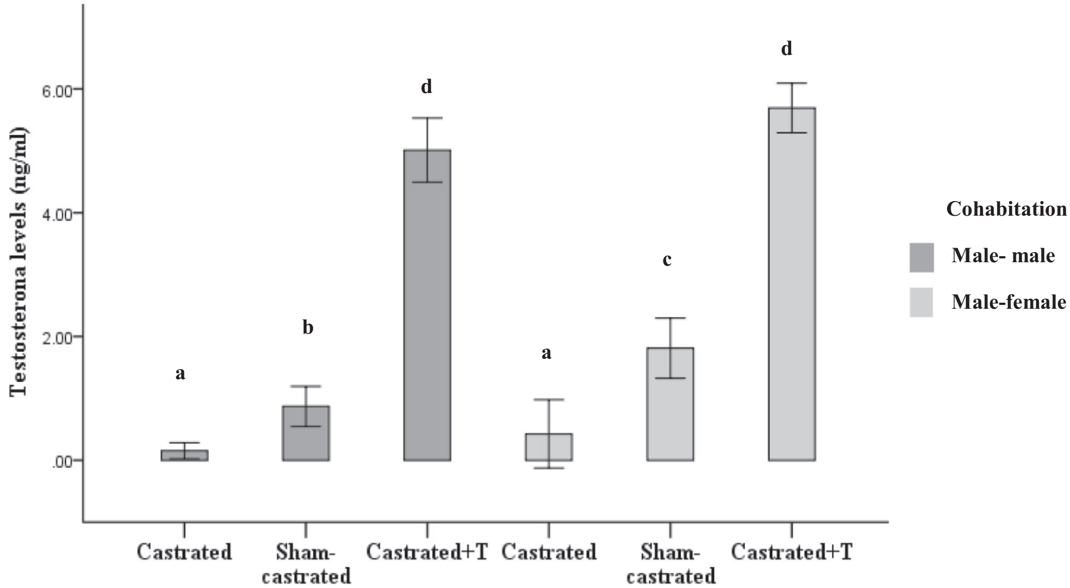

Fig. 2. Cohabitation with a female caused a significant increase in T levels in sham-castrated males, but this was not observed in the sham-castrated males that cohabitated with a male. Data are represented in means and SE. The letters indicate significant differences.

et al., 1999; Matsumato et al., 2005; Lürzel et al., 2011). In several species of avian and mammalian, it has been shown that T is required for exhibition of aggressive behavior; castration caused a significant decrease in circulating T and the subsequent elimination of territorial aggression, whereas T replacement restores this behavior (Barfield et al., 1972; Christie and Barfield, 1979; Koolhaas et al., 1980; Albert et al., 1986).

These results also indicated that although T is required for displaying territorial aggression, the exhibition of this behavior is dependent on social conditions; thus, the sham-castrated males and castrated males with T replacement in the male-male cohabitation did not display aggression as the males in cohabitation male-female, even though T was present. This would indicate that cohabitation with a female is a social factor that modulates the exhibition of territorial aggression. In the laboratory rat, territoriality is strongly enhanced by cohabitation with a female (Rosvall and Peterson, 2014). Male prairie voles (*Microtus ochrogaster*) that were pair-bonded for two weeks displayed intense levels of aggression in tests of resident-intruder (Kyle et al., 2007). The effect of the cohabitation with a female on territorial aggression in the male of the Mongolian gerbil may be mediated by an increase in T concentrations because sham-castrated males that cohabited with their mates had peripheral concentrations of T significantly higher than those sham-castrated males that cohabited with a male. Then, the increase in testosterone is caused by social context, in this case, cohabitation with a female. The increase in T could be part of the mechanism that gives the male the ability to defend his territory. However, it seems that is not the only one, since castrated males with T replacement that cohabited with a male, although they had T levels significantly higher than those of the sham-castrated males that cohabited with a female, were not aggressive. We think that the cohabitation with a female causes other neuroendocrine changes, in addition to an increase in T, that stimulate territorial aggression. For example, neural activation; in the Mongolian gerbil, mating, specifically copulation causes the activation of the posterodorsal preoptic nucleus, the lateral part of the posterodorsal medial amygdala, and the medial part of the medial preoptic nucleus. In Syrian hamster (*Mesocricetus auratus*) mating and aggressive behavior both activated neurons in the anterodorsal and posteromedial bed nucleus of the stria terminalis, paraventricular and ventromedial nuclei of the hypothalamus (Kollack-Walker and Newman, 1995). Despite that in this study, copulation was not observed, males in cohabitation with a female copulated because females got pregnant. In the laboratory rat, single copulation increases the intensity of attack and decreases the latency of onset of aggression (Flannelly et al., 1982). In other rodents as the laboratory mouse and deer mice (*Peromyscus maniculatus*), the mating also facilitates aggression (Dewsbury, 1984).

The peripheral concentrations of T and the attack latencies of the sham-castrated males that cohabited with a female were not correlated. Further, the level of aggression between sham-castrated males and castrated males with T replacement in male-female cohabitation was similar, although the latter had significantly higher T concentrations. These results suggest that territorial aggression in the Mongolian gerbil may be displayed for T levels ranging from small increases of T to concentrations that exceed the physiological range, once the aggression has been triggered by the social context, as cohabitation with a female. In the laboratory rat, the frequency of aggression was correlated with the T serum concentrations up to the normal level, but territorial aggression was not enhanced when serum T concentrations were raised above the normal baseline levels (Albert et al., 1988; Albert et al., 1990).

These results suggest that T is involved in the mechanisms that regulate territorial aggression in the male Mongolian gerbil, and the cohabitation with a female is a modulator of this behavior.

Futures studies could investigate the role of other neuroendocrine changes, further of an increase in T associated with mating in the regulation of the territorial aggression, in this rodent.

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