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Dominant–subordinate relationships in hamsters: Sex differences in reactions to familiar opponents

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Abstract

In the majority of mammalian species, males are dominant over and more aggressive than females. In contrast, some reports suggest that female golden hamsters are more aggressive than males but systematic comparisons using the same methods for both sexes are rare. We observed same-sexed pairs of hamsters over repeated trials to assess whether sex differences existed in the level of agonistic behavior and in the development and maintenance of dominant–subordinate relationships with familiar partners. There were no sex differences in measures of agonistic behavior or fear responses (fleeing) during the initial series of three trials on the first day of testing. Following a four-day interval, males that had lost in session 1 showed fearful responses to a familiar dominant male and were not likely to engage in a fight with him. In contrast, females that lost the initial fights were not fearful and fought vigorously with the familiar winner in subsequent encounters. Although the amount of agonistic behavior engaged in by females did decrease over the course of the three sessions, females that lost did not demonstrate an increase in fear, as measured by the latency to flee. Males that lost fights did show increased fear during later trials and sessions. These results suggest that female hamsters are less affected by losing fights than males are and thus that females are less likely than males to develop highly polarized dominant–subordinate relationships. Further work is needed to understand the mechanisms underlying these sex differences.

Keywords: Hamster; Aggression; Sex differences; Behavior; Fear; Anxiety; Dominance

Introduction

The agonistic behavior of hamsters has been well described, starting with a study by Melton (1950). Both male and female hamsters have been shown to reliably engage in intense agonistic behavior during same-sex encounters (Payne and Swanson, 1970; Takahashi and Lisk, 1983). Fighting in both sexes is affected by numerous factors, including (a) the hormonal status of the subject (Meisel et al., 1988; Payne and Swanson, 1971a,b,c; Takahashi, 1990; Vandenbergh, 1971), (b) the hormonal status of the opponent (Kislak and Beach, 1955; Marques and Valenstein, 1977; Payne, 1974), (c) changes in photoperiod (Garrett and Campbell, 1980; Jasnow et al., 2002; Landau, 1975), (d) prior housing conditions (Payne, 1973; Wise, 1974), and (e) the size and complexity of the testing environment (Johnston, 1975a,b; Payne, 1973; Payne and Swanson, 1970). A single intra-sexual agonistic bout progresses through a well defined and restricted set of stereotyped behaviors, including investigation, offensive and defensive posturing, and actual fighting, during which the two individuals are oriented at right angles to one another and attempting to bite one another, a "rolling fight" (Floody and Pfaff, 1977). Descriptions of the behaviors and sequences of behaviors used in fights have been thoroughly documented (Grant and MacKintosh, 1963; Johnston, 1976; Lerwill and Makings, 1971; Floody and Pfaff, 1977). A single fight typically results in a clearly identifiable winner and loser (Payne and Swanson, 1970) with the loser attempting to flee from the winner and the test area. Once a male subject defeats an opponent, the relationship established in the initial fight is usually maintained in future encounters between that pair of males (Floody and Pfaff, 1977; Johnston, 1975a,b; Payne and Swanson, 1970).

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Nonetheless, it is still not clear whether sex differences exist in the intensity or duration of fights or in the effects of winning or losing on the subsequent behavior of participants. This is because few studies have used the same methods to directly compare the behavior of males and females. Payne and Swanson (1970) showed that in same-sex encounters males and females did not differ in levels of agonistic behavior but there was a high degree of variability in female agonistic behavior over the estrous cycle (see also Lisk and Nachtigall, 1988; Takahashi and Lisk, 1983, 1984). Since the studies by Payne and Swanson (1970), other researchers have described females as being more aggressive than males. These claims were based on results showing that females were dominant over males and on observations indicating that females were more likely to cannibalize nests of other females than males (Brain, 1972; Floody and Pfaff, 1977; Goldman and Swanson, 1975a,b; Marques and Valenstein, 1977; Payne and Swanson, 1970; Tiefer and Johnson, 1975). In addition, in some studies, subjects were housed in groups, a procedure that increases aggression in females and increases indicators of social stress in both sexes, (e.g., changes in adrenal weight and total body weight; Gattermann et al., 2002). Thus, due to the variability of the methods used, the lack of careful comparisons using the same methods, and in some cases the lack of controlling for the reproductive state of females, sex similarities, and difference in agonistic behavior are not clearly understood.

Males and females do appear to differ in the development of and long-term physiological and behavioral reactions to fighting, particularly in the responses of losers and their subsequent reactions to stimulus animals. Potegal et al. (1993) showed that, after a single, prolonged bout of agonistic behavior, nearly 90% of defeated males displayed submissive postures when presented with a novel, non-aggressive stimulus male, an effect called conditioned defeat. Recently, it was shown that females do not show the same level of conditioned defeat (Huhman et al., 2003). This sex difference in behavioral response was present despite similar increases in adrenocorticotropic hormone (ACTH) in both males and females. In this study, there were four relatively long aggressive interactions (5 min) and a single test trial with a novel stimulus animal. The behavior during fights, however, was not reported, and thus it is not known whether the differences observed between males and females in response to a non-aggressive intruder were due to differences in levels of aggression during the initial fights. Work by Taravosh-Lahn and Delville has recently shown that sex differences do exist in the development of adult-like aggression and the response of juvenile animals to social subjugation. Females have been shown to develop adult-like attack styles earlier in life than males and they are less affected by early social defeat than males are. These data suggest that sex differences in aggression and responses to agonistic encounters are present early in life (Taravosh-Lahn and Delville, 2004). Previous studies with adult hamsters, however, showed no sex differences in measures of aggressive behavior in like-sex encounters (Floody and Pfaff, 1977). The females used in the studies by Floody and Pfaff were tested across all 4 days of the estrous cycle and were subjected to different housing conditions compared to males. Thus, no firm conclusions can be reached about sex differences in agonistic behavior or the effects of fighting on later responses to familiar or novel individuals.

In this paper, we took a systematic approach to study like-sexed agonistic encounters in golden hamsters. We compared interactions in pairs of males and pairs of females over 3 encounters during a single day and during additional interactions 4 and 8 days later. We recorded behaviors that occurred during these like-sex encounters and assessed the (a) level of agonistic behavior in male–male versus female–female encounters, (b) fear responses to a known winner and (c) the level of fear responses over days. Unlike all previous studies, the end of each fight was determined by the behavior of the animals (one animal fleeing), making these agonistic encounters more similar to those observed in the wild (Johnston, unpublished observations).

Materials and methods

Subjects

Subjects were 26 adult male and 30 adult female golden hamsters (*Mesocricetus auratus*) weighing between 140 and 190 g that were born and raised in the laboratory. This colony is derived from and periodically bred with new stock from Charles River, Inc. Female subjects were intact and had normal estrous cycles. Sexual receptivity (estrus) was assessed by testing for lordosis in response to males and sometimes by assessing the consistency of the vaginal secretion (Orsini, 1961). Normal cycling was insured by repeated testing of females for at least 1 month prior to use of the animals as subjects. We used females that were 1 day pre-estrous because in pilot studies females during this part of the estrous cycle demonstrated the highest levels of agonistic behavior toward each other (Floody and Pfaff, 1977; Kislak and Beach, 1955; Takahashi and Lisk, 1983, 1984). Thus, if females are more aggressive than males, they should definitely demonstrate it in these interactions. All hamsters were born in the colony, weaned at 28–30 days, and housed individually after weaning. They were maintained on a reversed 14:10 light–dark cycle; food and water were available in their cages at all times. As part of standard laboratory procedures, all animals received minimal social experience with other males and females during their first 3 months of life; this consisted of placing male and female juveniles into a testing arena divided into 4 compartments by a wire-mesh barrier on two separate days for 5 min on each occasion. This allowed social investigation to occur but did not permit fighting or mating. Some of the hamsters used in this study had been previously used as scent donors or as stimulus animals in open field tests 1 month or more before this experiment.

Ethical note

Animal care was in accordance with Cornell University IACUC and FDA standards. Veterinarians were continually available in the case of injury. Our protocol required that, if an animal were injured during testing, that animal would be removed from the study and receive immediate medical attention. No animals were injured or removed from the study.

Testing procedure

Male and female hamsters were tested during the first 2 h of the dark portion of their light:dark cycle; illumination was provided by a 25 W bulb 10 ft distant and pointed away from the arena. There were three sessions over a period of 9 days, with four-day intervals between sessions (tests occurred on Day 1, Day 5 and Day 9). This schedule allowed us to test females three times on the same day of their cycle. Each session consisted of three trials separated by four-minute intervals (Fig. 1). Two male or two female hamsters were placed simultaneously into a neutral testing arena and were allowed to interact. A trial was over when one of the animals jumped from the arena, made three successive attempts to