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Re-feeding and the restoration of odor attractivity, odor preference, and sexual receptivity in food-deprived female meadow voles

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Abstract

Food-deprived meadow voles were used to test predictions of two hypotheses associated with the recovery of sexual behaviors following re-feeding. Specifically, we tested between the body weight set point and metabolic fuels hypotheses. To do so, we determined whether the body weight of previously food-deprived female voles had to return to pre-food deprivation levels before they would recover their sexual behaviors. The body weight set point hypothesis predicts that food-deprived females that were re-fed will recover their sexual behavior after they return to their original body weight. In contrast, the metabolic fuels hypothesis predicts that food-deprived females that were re-fed will recover their sexual behavior before they return to their original body weight. That is, when the females are in positive energy balance. To distinguish between these two hypotheses, female voles were food deprived for 24 h, which is sufficient to inhibit all three components of sexual behavior. The food-deprived females were then supplied ad libitum food for 0 h, 24 h, 48 h, 72 h, or 96 h and weighed. Females were then tested for their sexual behaviors (odor attractivity, odor preference or proceptivity, sexual receptivity). Re-feeding for 48 h was sufficient to restore odor attractivity, 72 h was sufficient to restore odor preferences for opposite sex conspecific odors, and 96 h was sufficient to restore sexual receptivity to those similar to that of females that were not food deprived. The time-points that the behaviors were recovered were prior to voles recovering their initial body weight. Thus, the data support the metabolic fuels hypothesis.

Keywords: Food deprivation; Re-feeding; Odor preference; Odor attractiveness; Sexual receptivity; Meadow vole

1. Introduction

Mammalian sexual behavior is limited by food availability [1]. This effect is more dramatic in female mammals than in males. The reason for this is that females invest more energy as compared to males in reproduction. Thus, the effects of food deprivation on sexual behavior have been almost exclusively studied in females [2]. Food deprivation or restriction causes inhibition of aspects of sexual behaviors in female Syrian hamsters (*Mesocricetus auratus*), rats (*Rattus norvegicus*), house mice (*Mus musculus*), musk shrews (*Suncus murius*) [3–5]. Recently, we have found that food deprivation among female meadow voles (*Microtus pennsylvanicus*) reduces or eliminates the three components of their sexual behavior, attractivity, proceptivity, and receptivity [6,7]. For rodents, sexual behavior depends on olfactory signals from the sender and responses by the receivers. Attractivity refers to the relative stimulus values of different senders of the same sex, when assessed by receivers of the opposite sex. Proceptivity refers to the sexually-appetitive responses of receivers to such odors of opposite sex conspecifics. Attractivity and proceptivity establish communication between potential mates, and allow them to coordinate behaviors that could facilitate or inhibit direct interactions [8,9]. In our previous study, we found that female voles lose the attractiveness of their odors to males (attractivity) after they are food deprived for 24 h. They also lose their

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preferences for male odors over female odors (proceptivity) after 6 h of food deprivation [7]. Finally, female voles lose their willingness to mate with males (receptivity) after 6 h of food deprivation (Pierce et al., submitted).

Despite a growing literature on the effects of food deprivation on the sexual behaviors of small mammals [4,10], much remains to be learned about the effects of re-feeding on the recovery of sexual behavior among female small mammals. Re-gaining access to food after a food deprivation restores reproductive physiology and mating behavior back to pre-deprivation levels in a number of species. For example, spontaneously ovulating rodents (Syrian hamsters, rats, and mice) typically inhibit sexual behavior and ovulation after a 48-h food deprivation that occurs immediately following a previous period of estrus. Regular cycles are recovered once the animals are re-fed for 48 h, and their estrous behavior and ovulation occur delayed by approximately the amount of time they were without food [1,4,5,11]. In contrast, female musk shrews that were food restricted for 48 h displayed estrous and proceptivity 1.5 h after re-feeding behavior [3]. However, time frames for recovery of sexual behaviors may differ between species and particularly among females that differ in reproductive physiology [4,10]. Thus, food-deprived females of different species may recover their sexual behavior at how long they have been re-fed. The time to recover their sexual behavior may be manifested in how long they need to be in positive energy balance prior to up-regulation of these particular behaviors.

It has been postulated that the occurrence of female fertility and sexual behavior in mammals depends on a female's body mass or percent body fat [12]. This is referred to as the body weight set point hypothesis [13,14]. In the context of our experimental design, this hypothesis predicts that food-deprived females that are re-fed will recover their sexual behavior after they gain a significant amount of body weight over their post-deprivation weights or return to their original body weights. However, in many species, females may be capable of displaying sexual behavior before they reach their original body weight, provided they are regularly eating and are in positive energy balance [4]. This phenomenon is explained by the metabolic fuels hypothesis. This hypothesis states that individuals must be at a sufficient level of oxidizable metabolic fuels to support fertility and sexual behavior [4]. In the context of this experiment, the metabolic fuels hypothesis predicts that food-deprived females that are re-fed will recover their sexual behavior before they return to their original body weight. That is, sexual behavior will be reinstated when the females are in neutral or positive energy balance.

The present experiments have three objectives. The first objective was to determine whether re-feeding restores the three components sexual behavior in food-deprived female meadow voles. Specifically, we determined the amount of time that it took food-deprived females to recover their attractivity, proceptivity, and receptivity after re-feeding. The second objective was to determine if these recovery times were similar for each component of sexual behavior. The third objective of the experiments was to determine whether the metabolic fuels hypothesis or the body weight set point hypothesis best explained the recovery of the sexual behaviors in female voles that were food deprived and then re-fed. To meet these objectives, we first food-deprived female meadow voles for 24-h food durations, an interval of time that is sufficient to inhibit attractivity, proceptivity, and receptivity. Next, we re-fed them with ad libitum food for 0 h, 24 h, 48 h, 72 h, or 96 h. We then tested the re-fed females for attractivity, proceptivity, and sexual receptivity at these re-feeding intervals.

2. Materials and methods

2.1. Animals

We used first- and second-generation laboratory born meadow voles derived from individuals captured at the Miami University Ecological Research Center (Oxford, OH). These captive voles were maintained from birth in either a long photoperiod (14:10-h L:D, lights on at 0700 h CST). We considered adult voles housed in long photoperiod as being reproductively active; like their free-living counterparts, these voles are attracted to the opposite sex and readily mate when paired with opposite sex conspecifics [14]. At 21 days of age, voles were weaned and housed with littermates in clear plastic cages (26×32×31 cm; l, w, h, respectively) containing wood chip bedding and cotton nesting material. We changed cotton nesting material and hardwood shavings weekly. At 42 days of age, voles were separated from littermates and singly housed in clear plastic cages (27×16.5×12.5 cm; l, w, h, respectively) for the duration of the experiment. All voles used in this study were 80–150 days of age, sexually naïve, and not previously food deprived. Female meadow voles do not undergo estrus cycles and all female voles were considered to have similar reproductive status; that is, they were not pregnant, lactating or both. To eliminate the potential for litter effects, we did not use more than two individuals from the same litter in any experimental group.

Four days prior to the start of the experiment, we measured daily the food consumption and body weight of the voles. We also weighed the voles before they were exposed to food deprivation, during food deprivation, during re-feeding, and immediately after testing was completed (see below for details of the tests). Body weights were taken at 0800 h each morning, except on the days when animals were tested, in which case, the body weight was taken at 1230 h CST.

During the experiment, food (Purina Rodent Diet # 5008, PMI Inc., St. Louis, MO, U.S.A.) and water were