



Sustained housing-type social buffering following social housing in male rats



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HIGHLIGHTS

- Social housing after fear conditioning induces housing-type social buffering.
- Social buffering was sustained for 12 h after a 12-h period of social housing.
- Social buffering was extended when the duration of social housing was increased.

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ABSTRACT

In social animals, recovery from the adverse effects of distressing stimuli is promoted by subsequent cohousing with a conspecific animal(s). This phenomenon has been termed housing-type social buffering. We previously found that social housing induced housing-type social buffering in fear-conditioned male rats. This buffering took the form of attenuated conditioned hyperthermia in response to an auditory conditioned stimulus (CS). Here, we assessed whether this social buffering is sustained even if the subject is housed alone after a period of social housing. When fear-conditioned subjects were housed alone during a 48-h period between conditioning and re-exposure to the auditory CS, they exhibited conditioned hyperthermia in response to the CS. However, conditioned hyperthermia was not observed when the 12-h period of social housing began 24 and 36 h after conditioning during the 48-h period. This was not the case when the 12-h period of social housing began 0 and 12 h after the conditioning. These results suggest that housing-type social buffering is sustained for 12 h after the 12-h period of social housing. We next considered whether increasing the duration of social housing would extend the period of social buffering. We observed social buffering of conditioned hyperthermia 24 and 48, but not 96 h after a 24-h period of social housing. These results suggest that social buffering was extended when the duration of social housing was increased. Taken together, our findings indicate that housing-type social buffering is sustained after a period of social housing.

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1. Introduction

In social animals, interactions with conspecifics can attenuate stress responses. In a phenomenon known as exposure-type social buffering, the effect of distressing stimuli is ameliorated when a subject is exposed along with a conspecific animal(s) [1]. Similarly, in housing-type social buffering, recovery from the effects of distressing stimuli is promoted by subsequent cohousing with a conspecific animal(s) [1]. For example, social housing was found to prevent weight loss [2] and increases in anxiety responses in the elevated plus-maze test [3] after social defeat.

Previously, we found that these two types of social buffering differentially attenuate stress and conditioned responses to an auditory

conditioned stimulus (CS) in male rats [4–6]. In our experiments, fear-conditioned rats exhibited robust freezing and conditioned hyperthermia, as well as activation of the hypothalamus-pituitary-adrenal (HPA) axis, when re-exposed to a CS that had been paired with a foot shock during fear conditioning. The observed freezing was blocked when a fear-conditioned rat was re-exposed to the CS with an associate rat. However, freezing was not affected when the rat was socially housed with an associate starting immediately after conditioning and then re-exposed to the CS in the absence of an associate. In contrast, social housing starting immediately after conditioning ameliorated conditioned hyperthermia in response to the CS, even if the rat was re-exposed to the CS unaccompanied by an associate. The presence of an associate in turn did not affect conditioned hyperthermia in response to the CS. Furthermore, HPA axis activation was suppressed by both manipulations, indicating that these phenomena can be considered instances of social buffering according to the proposed definition [1]. Taken together, these data indicate that exposure-type and housing-

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type social buffering can ameliorate conditioned fear responses and conditioned hyperthermia, respectively.

In our subsequent analyses, we identified several characteristics of housing-type social buffering. For example, in housing-type social buffering, social housing does not need to commence immediately after fear conditioning. Specifically, we found social buffering of conditioned hyperthermia in animals tested after 18-, 12-, or 24-h of social housing that had commenced 6, 12, or 24 h after conditioning, respectively [7]. In addition, a study in which the subject and accompanying rat were separated by a wire mesh partition during social housing indicated that physical interaction is not necessary for the induction of housing-type social buffering [8]. Immunohistochemical analyses identified several brain regions that might be involved in the induction of social buffering [8]. However, in all of our previous studies, the subjects were re-exposed to the CS immediately after social housing. Therefore, whether social buffering is sustained if a subject is alone for a period of time after social housing is unclear. Additionally, whether the duration of social housing affects the subsequent sustainment of social buffering is unknown.

To address these questions, we conducted a study in which a fear-conditioned subject was re-exposed to the CS 48 h after conditioning. During this 48-h period, the subject was socially housed with another rat for 12 h starting 0, 12, 24, or 36 h after conditioning. We measured body temperature in response to the CS to evaluate social buffering of conditioned hyperthermia. Although housing-type social buffering has not been found to affect freezing behavior [5,7,8], we simultaneously observed this behavior to confirm successful fear-conditioning. We next assessed whether 24-h of social housing continued to induce social buffering 24, 48, or 96 h after social housing had ended.

2. Material and methods

2.1 Animals

All experiments were approved by the Animal Care and Use Committee at the Faculty of Agriculture, University of Tokyo, based on guidelines adapted from the "Consensus Recommendations on Effective Institutional Animal Care and Use Committees" from the Scientist Center for Animal Welfare.

Experimentally naïve male Wistar rats (aged 7.5 weeks) were purchased from Charles River Laboratories Japan (Kanagawa, Japan). They were housed 3–4 animals per polycarbonate cage (28 × 44 × 20.5 cm) in a controlled colony room with an ambient temperature of 24 ± 1 °C and humidity of $45 \pm 5\%$. Food and water were available *ad libitum*. The animals were maintained under a 12-h light/12-h dark cycle (lights switched on at 08:00). Each rat was assigned to either the subject or the associate group, and cage mates were assigned to the same group to maintain unfamiliarity between the subject and associate rats. Associate rats were housed individually in a colony room for 3 days before the first day of social housing with the subject rats. During this period, the associate rats were handled for 5 min per day. Each associate rat was used only once.

2.2 Experiment 1

The general procedures were the same as those described in our previous studies [5,7,8]. Briefly, 1 week before the conditioning day, all subjects were anesthetized with isoflurane and intraperitoneally implanted with a telemetry transmitter (TA10TA-F40; Data Sciences International, St. Paul, MN). After the surgery, the subjects were housed individually and handled for 5 min per day for 3 days before the conditioning day. Two days prior to the conditioning day, the subjects' home cages were moved from the colony room to an experimental room where they were placed on an antenna board (RLA1020 RPC-1; Data Sciences International) in a soundproof chamber (36 × 54 × 35 cm; Muromachi Kikai,

Tokyo, Japan). The experimental room had a constant temperature (24 ± 1 °C) and a 12-h light/12-h dark cycle (lights on at 08:00).

We conducted fear conditioning in an illuminated conditioning room between 09:00 and 18:00. On the conditioning day, each subject was individually brought into the conditioning room and placed in an acrylic box with a metal grid floor (28 × 20 × 27 cm). During a 15-min conditioning period, the subjects in the conditioned group received five repetitions of a 3-s tone (1 kHz, 80 dB) that terminated concurrently with a foot shock (0.5 s, 0.6 mA). For rats in the non-conditioned group, we presented the CS and foot shock separately during a 15-min period. The inter-trial interval randomly varied between 60 and 240 s.

We conducted the fear-expression test 48 h after conditioning. In the alone situation, the conditioned and non-conditioned subjects spent 48-h alone in a polycarbonate cage with clean bedding (non-conditioned, $n = 6$; conditioned, $n = 6$). In the social situation, a subject was housed alone for 36, 24, 12, or 0 h immediately after conditioning and then socially housed with an associate for 12 h. The subject was then housed alone for 0, 12, 24, or 36 h until the fear-expression test (Fig. 1A). Therefore, the conditioned subjects underwent the fear-expression test 0 (0h alone, $n = 8$), 12 (12h alone, $n = 8$), 24 (24h alone, $n = 8$), or 36 (36h

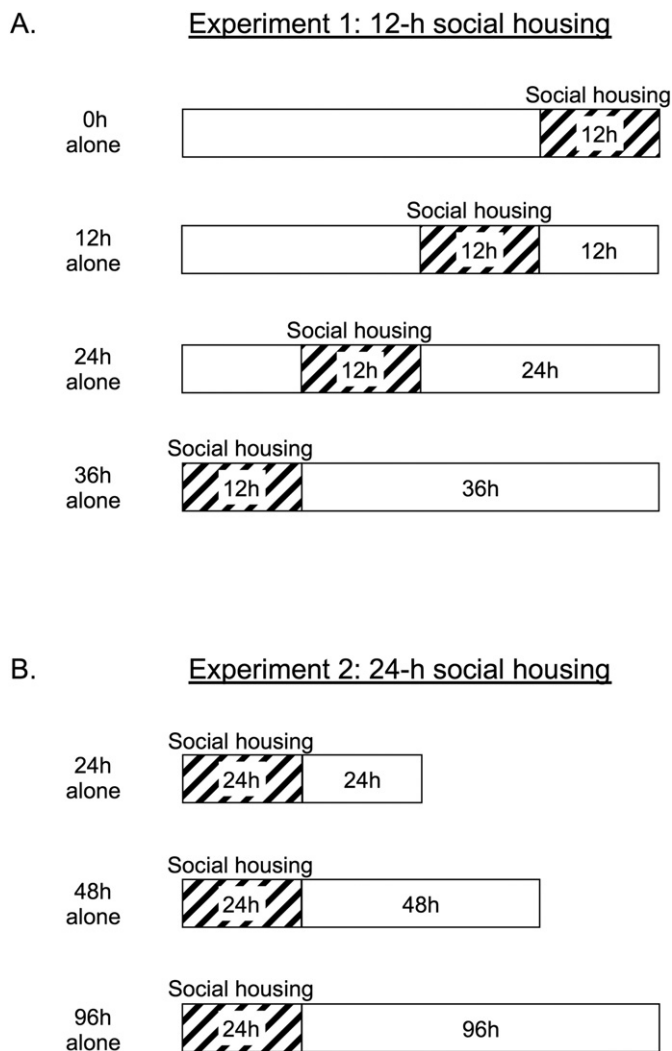


Fig. 1. Schematic diagrams of the experimental procedures. (A) In experiment 1, the subject was housed alone for 36, 24, 12, or 0 h immediately after conditioning and then socially housed with an associate for 12 h. The subject was then housed alone for 0, 12, 24, or 36 h until the fear-expression test. (B) In experiment 2, the subject was socially housed with an associate for 24 h immediately after conditioning. The subject was then housed alone for 24, 48, or 96 h before being subjected to the fear-expression test. Open and shaded squares indicate the period of individual housing and social housing, respectively.

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