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Research report

Observational threat conditioning is induced by circa-strike activity burst but not freezing and requires visual attention

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ABSTRACT

Social transmission refers to a process in which an observer (OB) acquires new information about the environment including threat situations, through the action of familiar conspecifics. Recently, a number of studies employing observational threat conditioning (OTC) in which OB mice expressed defensive responses following indirect exposure to pair-housed partner mice (demonstrator: DE) which were receiving repeated footshocks, have produced interesting insights into the social mechanisms of emotional transfer. However, the nature of the transmitted information or the critical cognitive processes involved in OTC is not clear. In a series of experiments, we investigated the key elements involves in triggering socially-induced defensive responses. In Exp.1, we compared the effectiveness in conveying a threat of two different types of defensive reactions of DEs: the circa-strike activity burst (CSAB) vs. freezing. The results show that the CSAB is more effective than freezing in inducing defensive freezing in an OB. In Exp. 2, we investigated different types of the OBs' defensive responses by measuring their change in head orientation or their "gazing" at the DEs, and their temporal synchrony with the DEs' defensive reactions in the form of their CSAB. The results show that OBs' gazing was significantly correlated with the DEs' CSAB, especially the DEs' jumping behavior, but not with the freezing of the DEs, indicating that jumping is a more effective trigger stimulus in inducing attentional capture in conspecific partner animals. In Exp. 3, the role of visual information was tested. The result shows that the OBs' level of freezing was significantly reduced when visual information was blocked by an opaque partition. In Exp. 4, to confirm the critical role of visual attention, we introduced distracting flashing lights, which were switched on and off at random intervals during the conditioning process. With all other conditions being maintained unaltered, the OBs in the distractor condition displayed a significantly decreased level of freezing, indicating that the visual attention paid to the DEs by the OBs during the conditioning process was critical for the social transmission of threat. Taken together, the results of the current study strongly suggest that socially transmitted defensive behavior is dependent on the specific behavioral elements of a DE's defensive behavior, and moreover, that a visual attentional process is required during the OTC.

1. Introduction

Various species of animal transmit information which is necessary for survival by interacting with conspecifics. For instance, animals can learn to select a nutritionally balanced diet or to avoid predators in unfamiliar situations on the basis of information gleaned from conspecifics [1]. In addition, animals develop defensive reactions more rapidly through the social transmission of threat signals in the form of the specific defensive behaviors of conspecifics that they observe [2]. It is widely known that humans and primates can develop aversive reactions against and, in some cases, phobias in relation to certain objects through observation [3]. Recently, the social transmission of threat has been increasingly studied in rodents. For example, in one study an observer mouse (OB) was able acquire the instinct to avoid biting flies by observing a model or demonstrator mouse (DE) suffering from the actions of the flies [4]. Furthermore, in observational threat conditioning (OTC) research, an experimental paradigm in which an OB is placed in a chamber adjacent to a DE while the DE is receiving repeated footshocks, it was possible to encourage defensive responses, particularly freezing, in the OB [5,6].

Previous studies have argued that an OB's freezing in the course of the OTC process is evidence of empathetic behavior (i.e. both the OB and the DE mice enter the same type of affective state). Additional evidence supporting this "empathy account" comes from the studies that have shown that the magnitude of observational fear response is a factor of familiarity [5,7]. For example, mice show a higher level of

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freezing when they observed a fear response of the cage-reared mice than the stranger during the conditioning [7]. The different housing history during the adolescent period modulates OTC in rats and mice [8,9].

The “empathy account” requires further specification, as it is not clear what type of affective state, whether pain or fear, is shared by DE and OB subjects. It is clear in DE that shock produces sharp somatosensory pain, and that the contextual cues associated with shock produce fear. If the OB is indirectly experiencing pain, it should display heightened pain sensitivity, while if it is experiencing fear, reduced sensitivity to pain or hypoalgesia [10]. The fact that the DE displayed a greater intensity of freezing indicates that their behavior might have functioned as a “sign stimulus” that triggered as particular defensive response in OB rather than provoking the “same emotional state.”

Additionally, the signs of pain-related fear in conspecifics were able to function as threat-associated signal cues to OBs. For example, pain or fear related chemosignals emitted or avoidance behavior displayed by demonstrator rodents induced pain-related analgesia or defensive avoidance behavior of conspecifics [4,10,11]. In this respect, it is critical to identify the perceptual and cognitive dimensions of DEs’ behavior that transmit a threat and elicit defensive behavior from OB. In the current study, a series of experiments was conducted in order to investigate the elements of this behavior that are essential to the triggering of socially-induced defensive responses. In particular, we focused on the two most distinctive types of threat-related behavior, the circa-strike activity burst and freezing.

2. Materials and methods

2.1. Subjects

In all experiments, male C57BL/6 N mice (8 to 9 weeks old; 24–30 g; Orient Bio) were pair-housed for 3 weeks (at 11 to 12 weeks old). The animals were maintained at 22 ± 1°C and 40–50 % humidity in a reversed 12-h light/dark cycle (light on at 9 p.m. and off at 9 a.m.), and were given access to food and water ad libitum. All behavioral tests were conducted during the dark phase of the cycle when the animals are normally active. All procedures followed the guidelines of “The Institutional Animal Care and Use Committee” from Korea University, Seoul, Korea.

2.2. Experimental apparatus

The apparatus for this experiment was employed according to the procedures described previously [5]. The apparatus consisted of two chambers (13 × 13 x 30 cm each), divided by a transparent Plexiglas partition. Each chamber contained a grid floor (1-mm-diameter rods, spaced 1 cm apart) connected to a scrambled shock generator (Coulbourn Instruments, Whitehall, PA, USA) for the delivery of footshock. The experimental apparatus was placed in a sound-attenuating cubicle (58 × 58 x 68 cm) equipped with a video camera and ventilation fan. The inside of the cubicle was dimly illuminated by a red acrylic-covered LED light (white, 50 lx). After each session, the chamber and the grid were cleaned with a 70% ethanol solution.

2.3. Experimental procedure: general method

The animals were handled gently for 5–10 min for at least 3 days before behavioral testing. Half of the mice in each group were designated as “demonstrator (DE)”, which were subjected to conditioning on day 1. The other half, designated as “observer (OB)” were placed in the adjoining chamber and allowed to observe the DE’s reactions to the footshock. For the conditioning process, a DE and an OB were individually placed in the two chambers (Fig. 2A). Following 5-min of

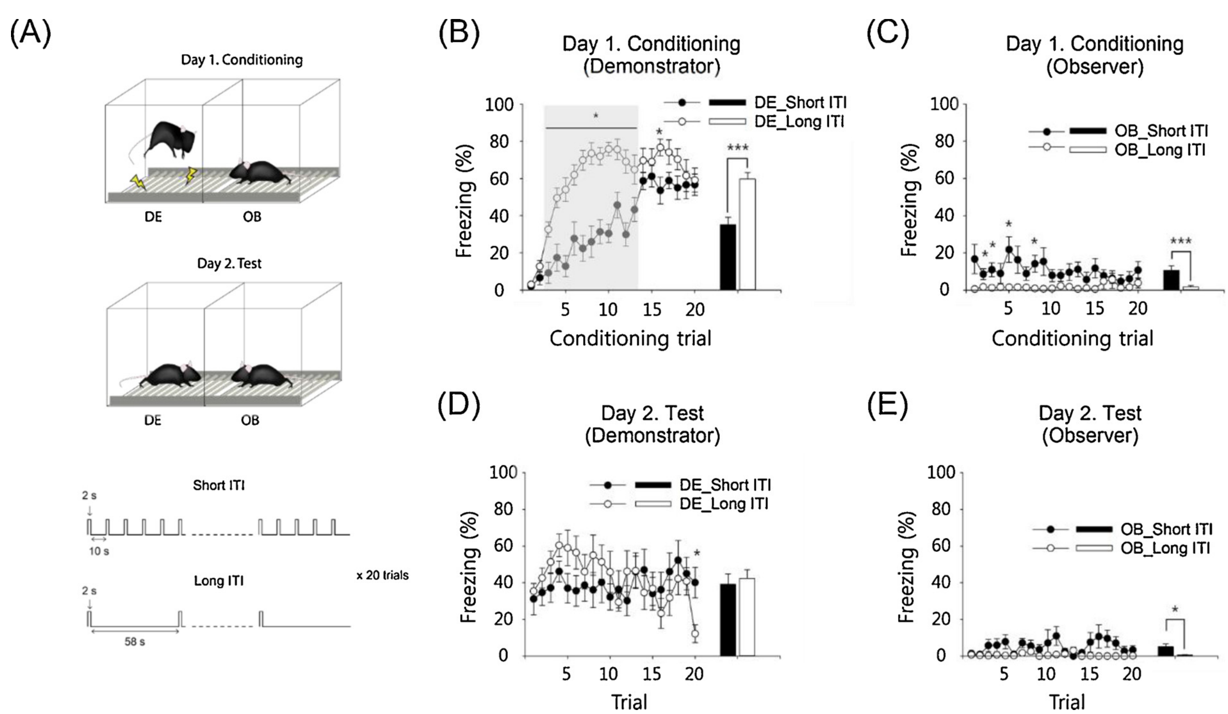

Fig. 1. The CSAB but not freezing of DE is critical to the socially-induced defensive freezing of OB. (A) Experimental procedure. To modulate the relative amount of the DE’s post-shock activity burst to freezing, two ITI durations were employed (Short vs. Long ITI, 12 s and 60 s respectively). During the conditioning, the OBs were allowed to observe the DE’s reaction to footshock (Day 1). During the test (Day 2), the OBs’ freezing level was measured in the presence of the DE. (B) Freezing during the conditioning (DE). During the conditioning, the DEs in Long ITI froze significantly more than the DEs in Short ITI (C) Freezing during the conditioning (OB). During the conditioning, the OBs in Long ITI showed froze significantly less than the OBs in Short ITI. (D) Freezing during the test (DE). Except for the last trial, during the test, the DEs in both groups displayed similar levels of freezing. (E) Freezing during the test (OB). During the test, the OBs in Long ITI displayed significantly lower levels of freezing than the OBs in Short ITI. (Gray shaded areas represent the statistically significant; * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$).