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Social inequality aversion in mice: Analysis with stress-induced hyperthermia and behavioral preference

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ABSTRACT

Humans have a sense of fairness and consequently are averse to inequality conditions. Recently, animal researchers suggested that some non-human animals also have inequality aversion. The author used stress-induced hyperthermia (SIH) to examine inequality aversion in mice. Experiment 1 measured the change in body surface temperature of mice under the condition of equality or inequality of food delivery. The results demonstrated that mice exhibited a large increment in body surface temperature when given a small piece of cheese and a cage mate was given a large piece. There was no increment in body temperature in equality conditions in which both the subject and the cage mate were given the same amount of cheese. The increase in body temperature was considered stress-induced hyperthermia caused by social inequality aversion. This is the first demonstration of inequality aversion of food delivery in mice. Simultaneous presentation of a large piece of cheese and a cage mate resulted in SIH in observer mice that were given a small piece of cheese, even though the cage mate was separated from the cheese by a partition to prevent it from eating the cheese. In Experiment 2, behavioral effects of inequality were examined in a chamber with two compartments. Mice could observe a cage mate in an adjacent compartment. They preferred a compartment with a cheese-eating cage mate to a compartment with cheese alone or cage mate alone. This result suggests inequality preference rather than inequality aversion. Thus, the results of Experiments 1 and 2 were contradictory. In a subsequent Experiment 3, both behavioral preference and body surface temperature were measured simultaneously. Mice stayed longer in the inequality condition compartment (cheese-eating cage mate), although inequality caused SIH. Supporting the results of both Experiments 1 and 2. Thus, social inequality induced stress (aversive property) but it also induced approaching behavior that might be maintained by the informative value of a food-eating cage mate.

1. Introduction

Inequality aversion is widely observed in humans and is an exciting topic of human social cognition (see Binmore & Shaked, 2010; Fehr & Schmidt, 1999, 2010) and also in social neuroscience (Shen, Jin, & Ma, 2013; Tricomi, Rangel, Camerer, & O'Doherty, 2010). There are two types of inequalities, namely disadvantageous and advantageous inequality. In human, disadvantageous inequality indicates that happy demonstrators cause negative emotions in observers, and advantageous inequality indicates that happy observers experience aversion when others are less happy. Humans have both types of inequality aversion but are more sensitive to disadvantageous inequality. Both types of inequality activate the same brain regions, such as the putamen, orbitofrontal cortex, and insula; analyses suggest that advantageous and disadvantageous inequality are dissociated connections among the structures and the amygdala (Yu, Calder, & Mobbs et al., 2014).

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Inequality aversion is also one of the most interesting topics in comparative cognition research (see Brosnan & de Waal, 2014; Watanabe, 2016a). The aversive property of inequitable outcomes has been demonstrated in several non-human primates (Brosnan & de Waal, 2014; Yamamoto & Takimoto, 2012); e.g., capuchin monkeys refused cucumbers when others obtained presumably tastier grapes instead of less tasty cucumbers (Brosnan & de Waal, 2003). However, various studies on inequality aversion in animals have reported contradictory findings (Bräuer, Call, & Tomasello, 2009; Sheskin, Ashayeri, Skerry, & Santos, 2014). For example, Sheskin et al. (2014) tested inequality aversion of capuchin monkeys in a no-cost situation and found no evidence of discrimination between equality and inequality conditions. Thus, small differences in procedure may affect the results. Most studies on inequality aversion are focused on primates; however, Range, Viranyi, and Huber (2009) and Range, Leitner, and Viranyi (2012) trained dogs to "give the paw" and then extinguished this behavior. Dogs displayed extinction of this behavior more quickly when trained with another dog that was rewarded than when trained alone with the experimenter, thereby suggesting "reversed empathy" or envious behavior. Recently, Oberliessen et al. (2016) examined inequality aversion in rats using a T-maze type choice paradigm. The rats preferred equal delivery of food to unequal delivery. Thus, rats also showed inequality aversion or equality preference.

Stress is known to raise body temperature (Houtepen et al., 2011). Various stressors have been reported to induce hyperthermia, including a novel cage (Pardon, Kendall, Perez-Diaz, Duxon, & Marsden, 2004), social threat (Keeney, Hogg, & Marsden, 2001), social defeat (Thornhill, Cooper, & Veale, 1979), and restraint (Marks, Vianna, & Pascal, 2009; Van der Heyden, Zethof, & Olivier, 1997; Van Eijl, van Oorschot, Olivier, Nijkamp, & Bloksma, 2006; Vianna & Carrive, 2005). The increment in body surface temperature is maintained by metabolic activity of brown adipose tissue (BAT) along the dorsal region of the body. Emotion-based thermoregulation of intrascapular BAT is controlled by the dorsomedial hypothalamus (DMH)-Raphe system (Lkhagvasuren, Nakamura, Oka, Sudo, & Nakamura, 2011; Morrison, Nakamura, & Madden, 2008).

I previously examined the social modification of stress in mice through stress-induced hyperthermia (SIH) measured using infrared thermography (Watanabe, 2015, 2016b). Mice restrained alone in cylinders had SIH; however, mice restrained simultaneously with other similarly restrained cage mates (equality condition) had lesser SIH, and mice restrained in the presence of free-moving cage mates (disadvantageous inequality condition) had the greatest SIH (Watanabe, 2015). These results are consistent with my earlier experiments that measured the memory-enhancing effects of stress and the stress-induced increase in corticosterone levels in exactly the same design of social equality and inequality conditions (Watanabe, 2011) and support the hypothesis that social inequality increases stress.

Types of inequality experiments vary between species. Primate researchers have employed disadvantageous inequality mostly in positive situations such as food delivery. One study with mice examined disadvantageous inequality aversion in negative situation (restraint stress) (Watanabe, 2011). However, disadvantageous inequality in a positive situation has not been examined in mice. Here, I examined the change in body temperature under social equality and inequality conditions of food delivery in mice. In the equality condition, the same amount of food was provided to two mice, whereas in the inequality condition, different amounts of food were provided to two mice.

2. Experiment 1: change in body temperature in equality and inequality conditions of food delivery

A pair of mice was tested in a chamber consisting of two compartments. The same amount of cheese was given to the two mice in the equality test, and different amounts of cheese were given to the two mice in the inequality test. Body temperature of the two mice was measured simultaneously.

2.1. Materials and methods

2.1.1. Subjects

Fourteen male C57BL/6J mice were used. They were 8–9 weeks old when the experiment started. The mice were housed four per cage (30 × 20 × 13 cm) with food and water freely available for more than 4 weeks before the start of the experiment. The hair on the dorsal part of shoulder was shaved under anesthesia (pentobarbital, 4.0 mg/kg i.p.). The temperature was kept at 24 °C, and the artificial light-dark cycle was reversed (12L:12D). Before the start of the experiment, cheese was given for 3 days in the home cages for adaptation to the cheese. All animals were treated in accordance with the guidelines of the Japanese Society of Animal Psychology, and the experiments were approved by the Animal Care and Use Committee of Keio University (No. 08011).

2.1.2. Apparatus

An experimental chamber, 19 × 11 × 20 cm, was made of transparent acrylic plastic. A partition was used to divide the chamber into two equivalent compartments of 9.5 × 11 cm. The partition was transparent acrylic plastic with a number of holes (diameter 0.5 cm and distance between the holes 0.3 cm) located 4.5 cm from the bottom, and the upper part was transparent acryl without holes. One mouse was placed in one compartment and another mouse was placed in the other compartment. In the cheese + mate condition, one compartment had a partition similar to that described above to separate a cage mate from cheese. A thermal image of each animal was recorded by an infrared thermal imaging camera (G100, NEC Avio). The distance between the camera and subjects was 60 cm. Body surface temperature was obtained from the thermal images using a software package (InfRecAnalyzer NS9500 Lite NS9500LT, NEC Avio). Details of the calibration and measurement have been described in Watanabe (2015). The highest temperature in a particular body surface area was obtained by drawing a rectangle around the shaved shoulder on the thermal image. The room temperature was maintained at 23 ± 2 °C, and the room humidity was 60–75%.