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A new method for studying social eavesdropping using male golden hamsters

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HIGHLIGHTS

- Social eavesdropping is used to acquire social information between conspecifics.
- A new behavioral model to study social eavesdropping in male golden hamsters
- The first study to demonstrate golden hamsters are capable of social eavesdropping
- Male hamsters can extract information from interactions between other conspecifics.
- Social eavesdropping and prior experience of defeat affect behavioral responses.

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ABSTRACT

Social eavesdropping is a special type of social learning and it is defined as the act of extracting information from social interactions between conspecifics. Social eavesdropping has advantages in information gathering and has attracted increasing attention. Emerging studies on social eavesdropping have been reported in several species, but the lack of suitable and manipulable laboratory rodent models remains a challenge to the study of the underlying mechanisms of social eavesdropping. The aim of this study was to take advantage of golden hamsters and their agonistic behaviors to develop a new laboratory method to study social eavesdropping. Male hamsters with or without a defeat experience were used as bystanders and were exposed to either a fighting interaction or a neutral encounter between two male demonstrators in a social learning chamber for a 3-day social learning. The behavioral responses of the bystanders toward observed demonstrators were tested in a U-shaped maze before and after the 3-day social learning. We found that (1) bystanders were attracted to the winning demonstrators in both short-term and long-term tests in experiment 1; (2) bystanders with a brief defeat experience displayed the opposite behavioral pattern and avoided approaching the winning demonstrator in experiment 2. It is evident that these hamsters acquired information about the relative qualities and dominance of the demonstrators and behaved differently toward different conspecifics afterward. Collectively, male hamsters are capable of social eavesdropping and prior experience of defeat has a significant impact on their consequent behaviors. Our newly developed behavioral method offers several advantages and it is useful for the study of social eavesdropping and its underlying mechanisms.

1. Introduction

Bandura's Social Learning Theory emphasized that people can learn from others' behavior, attitudes, and outcomes of those behaviors via observation, imitation, and modeling [1]. Social learning is a special type of learning ability and cognitive function. Many animals are also capable of learning not just from their own experiences, but also learning from the experiences of others. The act of gathering information from interactions between other conspecifics without taking part in them has been termed 'social eavesdropping' [2–4]. By witnessing such interactions, a bystander might learn and acquire information from the signalers and then use that information in the future. The use of the term eavesdropping dates back to animal studies from three decades ago but the concept of social eavesdropping and its explicit definition appeared only in the last decade of the 20th century [3,4]. Social eavesdropping has the advantage that information about the relative qualities of the conspecifics can be gained without the need to engage in costly and dangerous interactions. In recent years, social eavesdropping has attracted increasing attention from behavioral scientists and evolutionary biologists, especially in the fields of territorial aggression, mate choice, and communication networks [5].

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Studies on social eavesdropping have been reported in several species, such as crayfish [6], teleost fishes [7], birds [8,9], dolphins [10], domestic dog [11], primates [12] and so on. The occurrence of social eavesdropping raises a number of interesting and important questions that remain much unclear. For example, the behavioral consequences after social eavesdropping and neural circuits of social eavesdropping remain much unknown. The study of this phenomenon and its underlying neural mechanisms is still in its infancy. The phenomenon of social eavesdropping has been widely reported in wild species. However, it is somewhat difficult to apply a well-controlled, systematic approach to investigate the neurobiology of social eavesdropping and to determine the causal effects of its mechanistic substrates, especially in wild species. Suitable animal models, particularly laboratory rodent models, are needed to further the understanding of the behavioral and neural mechanisms of social eavesdropping.

Among small experimental rodents, golden hamsters (*Mesocricetus auratus*) are a classic model used for investigating the behavioral, pharmacological, hormonal, and neurobiological mechanisms of social interactions and social defeat [13–17]. Golden hamsters are territorial animals that defend their territories from overlapping neighbors and other intruders [18,19]. They are widely used for behavioral and stress-related studies in the laboratory and in the field [13,19,20]. The experience of social defeat, a stressful experience with high ecological and ethological validity compared to other stressors used in the laboratory, has frequently been applied to hamsters to investigate the behavioral, physiological, hormonal, and neurobiological mechanisms of social conflict [17,21–23], as well as of social learning and memory [14,24,25]. Indeed, the experience of social defeat in hamsters is sufficient to generate long-lasting and context-specific submissive behaviors towards specific opponents, and the formation of long-term (from 1 to 7 days) social memory requires *de novo* protein synthesis [26,27]. Several brain areas were also revealed to be involved in the recognition of familiar individuals by defeated hamsters [14,17]. These studies indicate that golden hamsters can be used as an animal model to study social defeat and social behaviors across different test contexts in the laboratory setting.

Given the increasing interest in social eavesdropping and the importance of social eavesdropping in higher cognitive functions and social interactions between individuals, it is of great interest to explore whether this social ability has evolved in golden hamsters and to develop a laboratory method to further study such a cognitive function in hamsters. In this study, we utilized the agonistic behaviors of male golden hamsters and designed two experiments to study social learning and its behavioral consequences in adult hamsters. In experiment 1, we examine behavioral consequences before and after social learning in naïve male golden hamsters. In experiment 2, we investigate the effect of prior defeat experience on social learning and consequent behaviors in defeated male hamsters. Findings from these two experiments can provide some empirical data to validate this new behavioral method and to support social eavesdropping in golden hamsters.

2. Materials and methods

2.1. Animals

Adult male golden hamsters (*M. auratus*), 4–6 months of age, without prior sexual or fighting experience were used as subjects in this study. Additional experienced males, 6–9 months of age, served as winning or losing demonstrators or used as stimulus males to minimize animal use. The experienced males encountered with either winning or losing experiences at least three times in the past one month and were trained with the same experience at least twice one week prior to the experimental sessions. The demonstrators were used to perform an act of social interaction (i.e., either a neutral encounter or a fighting interaction) to ensure social learning and to facilitate behavioral responses for each subject. All of the hamsters were descended from the stock of the National Laboratory Animal Center in Taipei, Taiwan, and, beginning at 2 months of age, were housed individually in Polysulfone individually ventilated cages (34 × 22 × 16 cm) that contained corn cob bedding in the animal rooms of the Psychology Department, National Taiwan University. Food and water were available *ad libitum*. The animal colony was maintained on a 12:12 light:dark cycle with lights off at 8 AM and a temperature of 22 ± 2 °C. Animals were handled and weighed daily beginning at least one week before the behavioral experiment. All of the animal procedures were performed according to protocols approved by the Institutional Animal Care and Use Committee, National Taiwan University.

2.2. Apparatus

A social learning chamber and a U-shaped maze were used in a set of two experiments in this study. Each apparatus was cleaned with 70% alcohol between each trial.

2.2.1. Social learning chamber

An acrylic social learning chamber was designed to investigate social learning from two types of social interactions. As illustrated in Fig. 1A, the social learning chamber was cuboid (26 cm long × 22 cm wide × 15 cm high) with a transparent plastic lid and consisted of two opaque, acrylic walls along the two long ends and two perforated, transparent screens (0.7 cm thick) along the two short ends. This chamber was divided into a demonstration compartment (15 × 22 × 15 cm) on one side of the chamber by the use of another perforated, transparent screen within the chamber, and two equally sized bystander compartments (11 × 11 × 15 cm), separated by an opaque acrylic wall on the other side of the chamber. The demonstration compartment allowed the two demonstrators to interact with each other within this area. Each of the two bystander compartments was connected to one of the perforated screens of the demonstration compartment and contained a metal mesh basket (8.5 × 8.5 × 14 cm) in which a male subject could be confined as a bystander during social learning. The walls on the outside ends of the two bystander compartments were also perforated so that air could be drawn through the entire social learning chamber from the demonstration compartment to the two bystander compartments by means of two electric fans mounted just outside the bystander compartments. The electric fans and complete setup of this apparatus were designed to minimize or eliminate any reciprocal interaction between the demonstrator and each subject and the possible interaction between the two subjects in the bystander compartments.

2.2.2. U-shaped maze

To evaluate behavioral performance before and after social learning, an acrylic U-shaped maze was designed to record subject's behavioral responses toward the demonstrator (Fig. 1B). The U-maze consisted of closed rectangular sections (10 cm wide × 15 cm high). The two arms of the maze were 99 cm long and were divided into three sections, the basal and distal sections of the arm (42 cm each) and the stimulus chamber (15 cm). Subjects had access to the two sections of the arm closest to the base of the maze but they could not get into the stimulus chamber. A stimulus chamber containing a mesh metal basket (8.5 × 8.5 × 14 cm), in which a male hamster could be confined as a stimulus male, was placed at the distal end of each arm. The base of the U was a triangle-shaped start section that was divided from the rest of the U-maze by two perforated opaque acrylic screens (10 cm wide × 15 cm high × 0.7 cm thick) that could be simultaneously removed to allow the subject into the maze. The walls on the outside ends of the two arms and start section were perforated so that air could be drawn through the entire maze from the two arms to the start section by means of an electric fan mounted just outside the start section. For the purpose of recording, the location of each subject was defined as the location of the subject's nose in the maze, and the maze was further divided into six sections: the distal and basal parts of the clear arm (with an empty mesh basket but no stimulus), the distal and basal