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Insights from rodent food protection behaviors

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ABSTRACT

This review aims to provide an update on the current state of research in food protection behaviors. This includes a detailed description of food protection behaviors, theoretical considerations, neuroscientific results, a separate examination of robbers' behaviors, and some suggestions on future studies. The goal is to provide a succinct overview of food protection behaviors while showcasing their usefulness through an ethologically gestalt lens in which to examine underlying systems of interest not only to better understand the species, but also as an antecedent for understanding human behaviors and conditions.

1. Introduction

Food protection behaviors have been used to explore cognitive and motor behaviors in rats from developmental, neurological, and social perspectives for nearly 30 years. This laboratory paradigm has been developed by Whishaw and Tomie originally for use as an ethological tool for investigating sensorimotor problems (Whishaw & Tomie, 1988). It has since revealed insights into development of sex differences in food protection behaviors, roles of hormones, sensory systems, neural systems, and cortical regions. Food protection behaviors have been discussed in terms of motor action patterns, interval timing theory, and mobility gradient theory. Although ethological researchers appreciate the diverse interpretations enabled by the study of natural behaviors, one of the goals of this review is to showcase the usefulness of food protection behaviors not only from an ethological lens, but also as a means to better understand human behaviors and conditions.

Recent neuroscience research with rats typically aim to model human clinical or neurological disorders by means of designs that enable precision and control (e.g., operant boxes, water maze). Natural behaviors however have their own merits, a large one being they do not require training or shaping. Psychology as a discipline has a torrid history of being "all or none". For instance, the years of debates on nature versus nurture. Now most psychologists appreciate that nurture works through what nature endows. Similarly, precision and control offer great starting points for understanding constructs but ecological approaches may provide unique insights into how animals function in more realistic situations. This review aims to offer more than a plea for these two perspectives to "play nice". Naturally occurring behaviors, such as food protection behaviors in rodents, occur spontaneously and are multifaceted, providing a rich context for careful analysis that is useful to ethologists as well as applied psychologists.

In this article, I review empirical studies examining food protection behaviors, discuss various methods of study, explore interpretations of converging results, and identify areas of future study. Although food protection behavior analyses enables

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specific hypotheses concerning individual constructs such as attention, memory, and motivation, it also enables researchers to evaluate whether holistic behavior and its neuroscientific basis is an interaction of many factors which may, in fact, differ than the sum of its parts.

2. Food protection behaviors description

Rats are opportunistic feeders, and most food is eaten but can be occasionally carried away. Whether food is eaten or carried away appears to depend on the familiarity and level of threat from conspecifics and/or predators (Whishaw, 1988). Indeed, since rats are opportunistic and eat where food is found, they appear to periodically stop to assess their safety. For instance, on a small stand in an open room, rats pause and use head movements during eating to look around lighted room every 2–3 s, even more often with larger food items. They also eat 20% more quickly in light during than in the dark (Whishaw, Gorny, & Dringenberg, 1991). Data suggests that food protection behaviors are only utilized if the robber is familiar and is deemed non-threatening (Whishaw & Tomie, 1987), which is consistent with expected behavior of territorial animals when confronted with an intruder (Adams, 1976; Blanchard, Blanchard, Takahashi, & Kelley, 1977; Whishaw, Oddie, McNamara, Harris, & Perry, 1990). In contrast, when approached by predators, rats appear more likely to engage in food carrying behavior (Whishaw et al., 1991).

Food protection behaviors involve movements that are constant and predictable, suggesting they are unconditioned, species-typical, stereotyped action patterns (Whishaw, 1988; Whishaw & Tomie, 1987). They include clearly identifiable elements such as the head, trunk, and paw movements, kinematic profile, and endpoint (Field, Whishaw, & Pellis, 1996). The vast majority of food protection behaviors have been published involving rat food protection interactions with conspecifics. Food protection behaviors initiate once the approaching rat ("robber") inserts its snout under the victim and attempts to grasp its food (Whishaw, 1988). Whishaw and Tomie suggest this may be adaptive insofar as the robber is then committed and a dodge will place it inconveniently behind the victim (Whishaw & Tomie, 1987). On over 93% (Whishaw & Tomie, 1987) of robbery attempts, the victim evades the robber using at least two different sequences of movement to protect their food, referred to hereafter as "dodging" and "bracing". Dodging is when the animal places the food item in its mouth to use all limbs to evade the robber. The movement is typically initiated with the forepaws then the contralateral rear limb, followed by the ipsilateral real limb to evade the robber, before transferring the food back to the forepaws to continue eating, although there are slight variations documented (Whishaw, 1988; Whishaw & Tomie, 1987). Bracing is when the animal continues to grasp the food by the front paws and merely rotates the body from the midsection to the head contralateral to the approach of the robber. Dodging results in a farther displacement. Dodging occurs approximately 78.3% of the time, whereas bracing occurs 21.7% of the time (Whishaw & Tomie, 1987). These behaviors are observed regardless of enclosure, from in housing cages, to small and large experimental enclosures (Whishaw & Tomie, 1987).

2.1. Methodological details

Various methods have been used to examine food protection behaviors. Through the testing duration, rats can be double-housed and maintained on a partial food deprivation schedule, to maintain body weight at approximately 90% of free feeding body weight. Before testing, rats are adapted to the apparatus, testing procedure, and food items to be used during the experiment. Rats are habituated until they continue eating even when another rat is placed in the enclosure. Rats are tested in pairs, with any pairing possibility (testing rats with their housemate e.g., (Whishaw & Gorny, 1994)), use of a dominant robber (Martin et al., 2008), or even a conspecific of the opposite sex (Field, Whishaw, & Pellis, 1997). The apparatus is typically made of a thin Plexiglas cylinder, approximately 40 cm in diameter and 45 cm high (e.g., (Martin et al., 2008; Whishaw & Gorny, 1994)). It is placed on a table with a clear glass top. An inclined mirror, through which the rats can be viewed and videotaped, is located underneath the table to enable the movements of the animals to be measured in two dimensions. See Fig. 1 for an example of the apparatus set-up.

A typical testing day consists of placing a rat (the victim) in the cylinder and then placing a food item on the floor in front of the victim so that it only has to walk forward to retrieve it. Once it begins eating, a second rat (the robber) is gently placed, facing the same direction, into the cylinder beside the victim. Thus, the robber need only walk forward to attempt to steal the food. Trials are video-taped until the food item is consumed. If the item is successfully robbed, the food item can be removed from the robber and either returned to the victim (e.g., to examine the time estimations and/or transition from dodging to bracing), or the victim can be given another food item (to maintain dodging vigor, particularly useful in unilateral neglect studies).

Kinematic analyses can further document motor abilities by means of average speeds during dodging and bracing behaviors as well as distance traveled by the victim during dodging and bracing. Distance and speed can be more easily quantified by digitizing food protection sequences using a motion measurement system, such as the Peak Performance Technologies, Inc. (Englewood, CO), which permits the digitizing of 60 fields per second. For motion analysis, the center of the food pellet in the mouth, the midbody, and the base of the tail are digitized in the victim (Pellis et al., 1996) or the tip of the snout, a mid-point along the longitudinal axis of the body, and the base of the tail (Field, Whishaw, & Pellis, 1997; Field, Whishaw, & SM, 1997). Depending on the goals of the study, the tip of the snout only is often used to examine robber behaviors, but three or more points can be identified if you are interested in studying the kinematics of the robber as well. See Fig. 2 for

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