



Operant behavior in dwarf hamsters (*Phodopus campbelli*): Effects of rate of reinforcement and reinforcer flavor variety

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ABSTRACT

We investigated operant behavior in a novel species, the dwarf hamster (*Phodopus campbelli*). In two experiments, hamsters were trained to lever-press for food reinforcement. In Experiment 1, rate of reinforcement was manipulated across conditions using four variable-interval schedules of reinforcement (delivering one to eight reinforcers per min). As predicted, within-session decreases in responding were steepest on the richest schedule. In Experiment 2, lever-pressing was reinforced by either a constant or a variety of flavored food pellets. Within-session decreases in responding were steeper when the reinforcer flavor remained constant than when it was varied within the session. In both experiments, subjects hoarded most reinforcers in their cheek pouches rather than consuming them in the operant chambers. These results are incompatible with post-ingestive satiety variables as explanations for within-session decreases in operant responding and suggest that habituation to repeatedly presented reinforcers best accounts for subjects' response patterns. Additionally, a mathematical model that describes behavior undergoing habituation also described the present results, thus strengthening the conclusion that habituation mediates the reinforcing efficacy of food.

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1. Introduction

Dwarf hamsters (*Phodopus campbelli*) are mouse-sized rodents found in sandy, arid regions of Siberia. Within the genus *Phodopus* (Latin for "hairy-footed hamster") are three species: *P. sungorus*, *P. roborovskii*, and *P. campbelli*. *P. campbelli* hamsters are often studied for their parental behavior. Compared to most rodent species, including other hamsters, *P. campbelli* males are highly paternal (Wynne-Edwards, 2003). They serve as midwives during the birth process, using their incisors and paws to help remove pups from the birth canal; they then lick their newborns' nostrils, facilitating the pups' first breaths (Jones and Wynne-Edwards, 2001). Fathers also retrieve experimentally displaced pups quickly (often within 10 s) and bring food to their offspring in their cheek pouches, sometimes after the mother has moved on to invest in a subsequent litter. Even under favorable laboratory conditions, pups rely on biparental care to survive (Wynne-Edwards, 2003).

The paternal behaviors of *P. campbelli* are well documented. Less is known about their learning abilities, although some recent studies have documented classical conditioning and foraging behaviors in this species. In an investigation of conditioned responding using

P. campbelli, subjects readily learned to approach and contact either a small cardboard square or a restrained conspecific signal for food. Conditioned responses directed toward the cardboard involved mainly gnawing, whereas social behaviors such as head and anogenital sniffs were elicited by conspecific signals for food (Lupfer-Johnson, 2008). Similarly, male dwarf hamsters attended to and sniffed their recently fed mates and learned to use which food their mates had eaten as a discriminative stimulus for which food was available in an open-field foraging task (Lupfer-Johnson et al., 2009).

Very little is known about *P. campbelli*'s operant behavior. Related Syrian hamsters (*Mesocricetus auratus*) have occasionally served as subjects in traditional operant paradigms (e.g., Anderson and Shettleworth, 1977; DiBattista, 1999), but to our knowledge, only one unpublished investigation of operant behavior in *P. campbelli* has been documented (Wertz, 2007). In Wertz's thesis, *P. campbelli* subjects were housed in operant chambers in a closed economy, so that all food was earned by lever-pressing on fixed-ratio (FR) schedules of reinforcement. Male and female hamsters performed similarly in terms of response rates and hoarding behavior. A tendency was noted in which subjects emitted more responses if the experimenter interfered with the accumulation of a hoard (i.e., by removing the hoard manually or by use of a wire mesh floor), but this tendency did not reach statistical significance. Finally, subjects increased their response rates as their ratio requirement increased from an FR 1 to FR 5, essentially earning the

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same number of pellets regardless of the schedule in effect (Wertz and Frieman, 2005; Wertz, 2007).

Wertz's (2007) study also reported that lever-pressing occurred in bouts over a 24 h period. Although large amounts of between-subject variability in the frequency and duration of lever-pressing bouts occurred, one pattern emerged: the size of the bout was directly related to the ratio requirement. That is, longer bouts of lever-pressing occurred on the larger ratios, and smaller bouts occurred when the ratio requirement was low. These results suggest that rate of reinforcement is an important variable governing operant behavior in dwarf hamsters. Although finding a relationship between rate of reinforcement and operant responding is not new (e.g., Herrnstein, 1970), it is the first time that the relationship has been reported with *P. campbelli*. What is not known, however, is how operant lever-pressing was temporally organized within the bouts. In traditional laboratory animals (e.g., rats and pigeons), it is well established that rate of operant responding often varies within an experimental session, particularly at high rates of reinforcement (e.g., McSweeney et al., 1996). Specifically, rate of operant responding increases, increases then decreases, or decreases within a standard operant conditioning session. Perhaps the most important variable governing the within-session pattern is rate of reinforcement. For example, higher rates of reinforcement produce steeper within-session decreases in responding than leaner rates of reinforcement (e.g., McSweeney, 1992).

The goal of the present project is to further explore bouts of operant behavior in *P. campbelli*. They are an appropriate species for the current research for several reasons. First, they readily forage for palatable reinforcers without food deprivation in an open field (Lupfer-Johnson et al., 2009). In addition, they store food in their cheek pouches. The food can be easily removed and quantified by an experimenter (Lupfer et al., 2003), and subjects typically do not consume reinforcers until back in their home cages (Lupfer-Johnson et al., 2009). This makes them an interesting species for studying theories of within-session changes in response rates. For example, one hypothesis suggests that within-session decreases in operant responding are related to post-ingestive satiety variables, such as cholecystokinin release, blood glucose, or stomach distension (Bizo et al., 1998). An opposing hypothesis suggests that habituation, defined as a decrease in responsiveness to a repeatedly presented stimulus (e.g., Thompson and Spencer, 1966), to the reinforcer modulates the within-session decrease in responding (McSweeney, 2004). Quantifying the number of food pellets hoarded in cheek pouches versus those consumed in a session enables investigation of the extent to which within-session changes in operant behavior may be related to post-ingestive satiety variables, or to a process that does not depend on ingestion, such as habituation.

In particular, the present study separated the predictions of habituation from the satiation explanation of within-session decreases in responding. The presence of habituation was established by testing for two of its fundamental empirical properties. Empirical tests were used because there is no generally accepted theory of habituation. Although many theories have been proposed (Sokolov, 1963; Wagner, 1976), none has been generally accepted (Mackintosh, 1987; Staddon and Higa, 1996). The present study tested for two fundamental properties of behavior undergoing habituation: *stimulus rate* and *variety effects*. The stimulus rate property of habituation refers to the finding that faster rates of stimulus presentation yield faster and more pronounced habituation compared to slower rates (Thompson and Spencer, 1966). To test the stimulus rate property of habituation, the rate of food presentation was delivered on four interreinforcer intervals: 7.5 s, 15 s, 30 s, and 60 s. It was predicted that within-session decreases in responding should be larger for the higher (e.g., 7.5 s) than the lower (e.g., 60 s) rates of food reinforcement.

A variety effect occurs when habituation is slower to stimuli that are presented in a variable, rather than a constant, manner. For example, Broster and Rankin (1994) showed that habituation of the tap withdrawal response in *Caenorhabditis elegans* proceeded more quickly when the taps were presented on fixed, rather than variable, interstimulus intervals. In the present study, variety effects were tested by keeping the flavor of the food reinforcer constant (i.e., bacon or chocolate), or by unpredictably changing the flavor of the food pellet, within an operant conditioning session. If habituation governs within-session decreases in responding, then these decreases should be larger when the flavor is held constant, than when the flavor is varied within the session. If satiation governs within-session decreases in responding, there should be no difference in the within-session pattern because the food pellets were identical in size (i.e., 20 mg) and nutritional content.

2. Experiment 1

The protocol to test the above questions was approved by the University of Alaska Anchorage Institutional Animal Care and Use Committee and conformed to the guidelines of the care and use of laboratory animals as required by the National Institutes of Health (National Research Council, 1996).

Experiment 1 was conducted to examine the within-session changes in subjects' rates of responding, relate those changes to rate of reinforcement, and measure the proportion of earned reinforcers which were consumed versus stored in subjects' cheek pouches. We hypothesized that dwarf hamsters would exhibit larger within-session decreases in response rates on richer (e.g., 7.5 s) than on leaner (e.g., 60 s) variable-interval (VI) schedules.

2.1. Method

2.1.1. Subjects

The subjects were 8 adult male dwarf hamsters (*P. campbelli*) bred from a colony acquired from Queen's University (Kingston, Ontario). The Queen's University breeding colony was created from wild-caught hamsters in Siberia (Wynne-Edwards and Lisk, 1987). Two 8-month-old subjects had previously served in an open-field foraging experiment (Lupfer-Johnson et al., 2009) and 6 1-month-old dwarf hamsters were experimentally naïve. At the beginning of the study, the mean weight of the subjects was 28.63 g ($SEM=3.17$). Subjects were housed individually in 26.67 cm × 48.26 cm × 20.32 cm plastic cages in a vivarium maintained at a temperature of 21 ± 1 °C. While in their home cages, subjects had free access to Mazuri® Rodent Pellets (PMI Nutrition International, LLC, Brentwood, MO) and water. Environmental enrichment (i.e., small cardboard boxes or paper bags) was added to each cage 1–2 times per week. The subjects were exposed to a 12:12 h light/dark cycle (lights on from 7:00 a.m. to 7:00 p.m.). To be consistent with previous work in our laboratory (e.g., Lupfer-Johnson et al., 2009), all sessions were conducted during the light portion of the cycle. Additionally, Wertz (2007) reported that operant lever-pressing in dwarf hamsters occurred during both the light and dark portions of the cycle.

2.1.2. Apparatus

The apparatus was a side-loading MED Associates (St. Albans, VT) two-lever operant conditioning chamber for mice, measuring 21.6 cm × 17.8 cm × 12.7 cm. A 2.5-cm × 2.0-cm food tray, which allowed access to chocolate flavored 20-mg dustless precision pellets (Bio-Serv®, Frenchtown, NJ), was centered on the front panel, 0.5 cm above the floor. Two 1.6-cm × 1.0-cm levers appeared 4.0 cm from this opening, one on each side. The levers, which required approximately 0.02 N for operation, were 2.2 cm above the floor and extended 1.0 cm into the enclosure. A 0.5-cm diameter yellow

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