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Research report

Effects of inter-food interval on the variety effect in an instrumental food-seeking task. Clarifying the role of habituation ☆

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ABSTRACT

Food variety increases consumption and the rate of instrumental behavior that is reinforced by food in humans and animals. The present experiment investigated the relationship between the variety effect and habituation to food by testing the role of the interval between successive food presentations on responding in an operant food-seeking task. Habituation to food was expected at short, but not long, interfood intervals. The effects of variety on food's long-term reinforcing value were also tested. Four groups of rats were trained to lever-press on different random-interval (RI) schedules of reinforcement to earn 45-mg food pellets. Half the rats in each group received an unpredictable mix of grain and sucrose pellets, while the other half consistently received sucrose pellets. Response rate began at a high rate and then decreased within each 30-min session for groups that received short inter-pellet intervals (i.e., RI-3 s and RI-6 s reinforcement schedules) but not in groups that received longer inter-pellet intervals (i.e., RI-12 s and RI-24 s). A variety effect in the form of higher responding in the mix group than the sucrose-only group was also only evident at the shorter intervals. Habituation and variety effects were also most evident with the short intervals when we controlled for the number of reinforcers earned, suggesting that they were not merely due to rapid satiation. The variety effect also appeared quickly when groups trained with longer inter-pellet intervals (RI-12 s and RI-24 s) were transitioned to shorter intervals (RI-3 s and RI-6 s). There was no effect of variety on resistance to extinction or on resistance to the response-suppressing effects of pre-session feeding. The results more clearly link this version of the variety effect to the short-term effect of variety on food habituation.

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Introduction

Appetitive behavior is stronger when organisms receive a variety of foods than when they receive the same food repeatedly (e.g., Raynor & Epstein, 2001; Remick, Polivy, & Pliner, 2009). This *variety effect* has been demonstrated in humans and animals when investigators have measured either food consumption or the rate of operant food-seeking behavior that is reinforced by food. One explanation of the variety effect is that variety slows habituation that can otherwise develop as a consequence of repeated presentations of the same food. *Food habituation* describes the reduction in eating that occurs as an eating episode progresses. When organisms are given the same food repeatedly, responding for it decreases (e.g., Epstein, Temple, Roemmich, & Bouton, 2009). Habituation may contribute to the cessation of eating within a meal. Variety may slow this process for several reasons (Bouton, Todd, Miles, León, & Epstein, 2013). For example, because habituated responding can "dishabituate" after a new stimulus (e.g., a new food type) is presented, providing one type of food might dishabituate suppressed responding to another food. Alternatively, because habituation is stimulus-specific, responding might recover whenever the food is changed. In addition, because habituation is slower when the habituating stimulus is distributed more widely in time, variety might slow habituation by increasing the interval between successive presentations of the same food. Any or all of these facts could contribute to a variety effect. However, we are not aware of any evidence to confirm that the variety effect occurs because of variety's specific effect on habituation. The purpose of the present research was thus to further examine the relationship between the variety effect and habituation to food.

The variety effect has been primarily studied in humans (Ernst & Epstein, 2002; see Epstein et al., 2009, for review). However, Bouton et al. (2013) recently studied the effect in an operant food-seeking

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task in rats. Using a method introduced by Aoyama and McSweeney (2001), they gave rats the opportunity to earn a 45-mg food pellet for every 4th lever press they performed in each of a series of daily 30-min sessions. After several sessions of training, responding began at a high rate at the start of each session and then declined through the remainder of the session, a result that was consistent with the possibility that the effects of the food pellet habituated within each session. Consistent with a variety effect, Bouton et al. found that presenting an unpredictable sequence of sucrose- and grain-based pellets slowed the decline in response rate that was otherwise observed when either pellet was presented exclusively. The effect became stronger over repeated sessions, as the within-session decline in responding deepened. That result is consistent with the possibility that the effect of variety on instrumental responding was due to its effect on habituation. However, enhanced responding for the mixture was also evident early in training, before the within-session decline became substantial. The fact that the phenomenon was evident so early leaves the possibility open that variety might also increase the reinforcing value of food in some manner that is separate from its effects on habituation. Although the results of at least one other study with animal subjects also suggests that variety can enhance responding in an operant task involving within-session decreases in responding (Lupfer-Johnson, Murphy, Blackwell, LaCasse, & Drummond, 2010), we are not aware of any evidence to suggest that food habituation is *necessary* to observe the variety effect.

Interestingly, Bouton et al. (2013, Experiment 2) also isolated a second "variety effect" that was not linked to within-session habituation. When rats were given alternating sessions that contained grain or sucrose pellet reinforcers consistently, the amount of responding for sucrose during sucrose sessions exceeded that observed in a control group that only earned sucrose pellets in every session. That effect was attributed to incentive contrast (e.g., Flaherty, 1996); exposure to a highly palatable food after exposure to a less palatable food can increase its positive effects. In this sense, variety can enhance responding between-sessions by virtue of a mechanism that is different from habituation. It is worth noting, however, that Bouton et al. (2013) also observed less responding to the grain pellet in the alternating group than in a group that received grain pellets consistently. Thus, the two pellets produced both positive and negative incentive contrast, and the average level of responding across sucrose and grain sessions was not different from that of the control animals.

The present experiment was designed to explore the role of habituation in producing the effect of variety on within-session responding in more detail. Most importantly, it was designed to separate variety's immediate effects on habituation from the possibility that it also has an impact on food's longer-term reinforcing value. As in the experiments of Bouton et al. (2013), rats lever-pressed to earn food pellets over a series of 30-min sessions. Different groups received either consistent sucrose pellets or an unpredictable mixture of sucrose and grain pellets. If anything, the present sucrose pellets are weakly preferred to the present grain pellets (Bouton et al., 2013; Winterbauer, Lucke, & Bouton, 2013). As a result, any demonstration of increased responding for the mixture of grain and sucrose pellets over sucrose pellets alone would provide a compelling demonstration of the variety effect.

To explore the role of habituation, different groups also earned the pellets at different rates: Pellets could be earned on Random Interval (RI) schedules of reinforcement that delivered pellets for the first response emitted after intervals averaging either 3, 6, 12, or 24 s since the last food pellet. The use of RI schedules, as opposed to the fixed ratio schedule used before (Bouton et al., 2013), provided better experimental control over the rate at which pellets were encountered. Because habituation generally occurs more quickly when the habituating stimulus is presented at high rates (e.g., Rankin et al., 2009), we expected that within-session habituation would be most pronounced with the higher rates of reinforcement. The question was whether the variety effect would also be most evident at those rates. If variety affects response rate by influencing the habituation process, a variety effect should be observed primarily in groups that otherwise demonstrate within-session habituation.

The experiment also included tests designed to assess whether variety affected behavioral persistence over and above its effect on within-session responding. After training with sucrose only or the sucrose/grain mixture, responding was tested (1.) during extinction, when pellet delivery was discontinued, and (2.) after satiation produced by free access to food immediately before a test session. If variety makes foods more reinforcing, it might increase behavior's resistance to extinction and/or resistance to satiation. Resistance to extinction and the effects of satiation have been considered indices of the reinforcer-produced "momentum" of operant behavior (Nevin & Grace, 2000).

Method

Subjects

Forty-eight naïve female Wistar rats purchased from Charles River Laboratories (St. Constance, Quebec) participated in the study. They were between 75 and 90 days old at the start of the experiment and were individually housed in suspended wire-mesh cages in a room maintained on a 16:8-hr light:dark cycle. Rats were maintained at 80% of their free-feeding body weights via small daily feeding of the maintenance chow, P500 Prolab RMH 3000 (PMI Nutrition International, Brentwood, MO).

Apparatus

The apparatus consisted of two unique sets of four operant conditioning chambers (Med Associates, St Albans, VT, model ENV-008-VP). All boxes measured 30.5 × 24.1 × 23.5 cm (length × width × height). The floor was made of stainless steel grids (0.48-cm diameter) and the ceiling and sidewalls were made of clear acrylic plastic. The front and rear walls were made of brushed aluminum. A recessed 5.1 cm × 5.1 cm food cup was centered in the front wall 2.5 cm above the floor. In both sets of boxes, a retractable lever (4.8 cm long and positioned 6.2 cm above the floor grid) was positioned 7.8 cm (center to center) to the right of the food cup. When extended, the lever protruded 1.9 cm from the front wall. Two 28-V panel lights (2.5 cm in diameter) were attached to the wall 10.8 cm above the floor and 6.4 cm to the left and right of the food cup. Ventilation fan provided background noise of 65 db.

The two sets of conditioning chambers had unique features that allowed them to be used as different contexts (Bouton et al., 2013; counterbalanced), although they were not used in that capacity here. In one set of four chambers, one acrylic plastic sidewall had black diagonal stripes, 3.8 cm wide and 3.8 cm apart. The ceiling had similarly spaced stripes oriented in the same direction. The floor grids were spaced 1.6 cm apart (center to center) on the same plane. The other set of boxes had no distinct visual cues, the floor grids were spaced 1.6 cm apart (center to center) and staggered such that odd- and even-numbered grids were mounted in two separate places, one 0.5 cm above the other. Each chamber in both sets of boxes was illuminated by one 7.5-W incandescent bulb mounted to the ceiling of the conditioning chamber, 34.9 cm from the grid floor, near the back wall.

There were two pellet reinforcers, both obtained from Test Diet, Richmond, IN, USA. One was a 45-mg grain-based food pellet (MLab Rodent Tablet [5TUM]), and the other was a 45-mg sucrose pellet (Sucrose Tablet [5TUT]). The different pellets were delivered by separate feeders that delivered the pellets to the same food cup. Previous research in this laboratory indicates little generalization between