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Motivational shift: Effects of unrestricted and restricted feeding on wheel running as an operant and reinforcing consequence on a multiple schedule of reinforcement

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ABSTRACT

Rats were exposed to a multiple schedule on which they pressed a lever on a variable-ratio schedule for wheel-running reinforcement in one component and ran a fixed number of revolutions for 15% sucrose solution reinforcement in the other component. Feeding was varied from restricted to unrestricted (ad-libitum) and then returned to restricted. Across these changes in feeding, average body weight varied from 262 g to 339 g to 258 g. Under ad-lib feeding, wheel-running and lever-pressing rates decreased while postreinforcement pause duration increased in the wheel-running reinforcement component. In the operant wheel-running component, wheel-running rates also decreased and postreinforcement pause duration increased. Notably, wheel-running rates in the operant running component were higher than in the wheel-running reinforcement component when rats were food restricted, but did not differ when rats were freely fed, indicating a reduced effectiveness of sucrose reinforcement. This reduction in response strengthening of operant wheel running by sucrose under ad-libitum feeding is consistent with a shift from food-related to intrinsic motivation of running. From a response deprivation perspective (Allison & Timberlake, 1974), this reduced effectiveness of sucrose reinforcement would occur if wheel running in freely fed rats became the more constricted behavior in the contingency between instrumental wheel running and contingent sucrose consumption.

1. Introduction

Behavior in the laboratory is often motivated by conditions related to the natural ecology of animals. On a multiple schedule of reinforcement, running in a wheel can function as reinforcement for behavior (e.g., lever pressing) in one component and as an operant that produces reinforcement (e.g., sucrose) in the other schedule component. As an operant, wheel running is increased by extrinsic reinforcement such as drinking sucrose, but as a reinforcing consequence wheel running is intrinsically motivated behavior with an automatic reinforcement function when made contingent on lever pressing, a low probability response (Belke, Mann, & Pierce, 2015). According to Belke and Pierce (2015), the automatic reinforcement function of wheel running can be altered by motivational manipulations involving response deprivation, either imposed by setting a contingency between the instrumental (operant) and contingent responses or by restriction of

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eating by withholding food (Allison & Timberlake, 1974). The objective of the current study was to investigate the effects of food restriction and body weight loss as a motivational operation for the automatic reinforcement effectiveness of wheel running. We used a multiple schedule in which wheel running was arranged as reinforcement for lever pressing in one component and as an operant producing sucrose reinforcement in the other.

Allison and Timberlake's (1974) response deprivation hypothesis is relevant to understanding behavior on a multiple schedule involving wheel running as an operant and as a reinforcing consequence. Response deprivation posits that, under unconstrained conditions, animals engage in behaviors at particular frequencies or durations referred to as the unconstrained baseline. When two responses are constrained to occur in a particular contingent relation on a schedule of reinforcement, the behavior that is more restricted relative to baseline (contingent response) should function to reinforce the less restricted behavior (instrumental response). Food restriction or withholding consumption of food is a motivational manipulation that would alter the response baselines of the contingent and instrumental responses. In addition, food restriction would be expected to alter the effectiveness of the contingency between the contingent and instrumental responses by increasing or decreasing the relative restriction of the two behaviors related by the reinforcement schedule.

Previous research has shown that food restriction accompanied by body-weight loss increases the probability of wheel running and operant responding for wheel running. Wheel-running rates vary inversely with food supply and body-weight level (Baumeister, Hawkins, & Cromwell, 1964; Collier, 1970; Jakubczak, 1967; Moskowitz, 1959; Price, 1976; Sclafani & Rendel, 1978; Treichler & Hall, 1962). Also, as body weight decreases with restriction of food consumption, wheel-running rate increases. Moskowitz (1959) showed that between 60% and 90% of normal weight, a −0.99 correlation obtains between wheel-running revolutions and percent of ad-libitum body weight. Similarly, Collier (1970) reported a −0.79 correlation between log body weight and log distance run over a 5–20% body weight loss in rats. Note, however, that this strong relation between body weight and wheel running does not typically emerge until rats have lost 10–15% of ad-lib weight (Sclafani & Rendel, 1978). Thus, in terms of response deprivation, mild food restriction and reduction of food consumption does not act as a motivational operation for unrestricted or baseline wheel running, but more severe food restriction does.

Over moderate to severe food restriction and weight loss, operant or instrumental lever pressing for contingent wheel running covaries with wheel-running rates (Belke, 1996, 2004). Belke (1996) showed that lever pressing for wheel running, on a series of response-initiated variable-interval (VI) schedules within a session, varied systematically with feeding required to maintain 80%, 100%, and 80% of an initial ad-libitum body weight. With free feeding and high body weight, both wheel-running and local lever-pressing rates decreased while postreinforcement pause (PRP) duration increased. Similar effects of restricted and unrestricted feeding have been observed for the reinforcement value of wheel running on progressive-ratio schedules. Pierce, Epling, and Boer (1986) investigated breakpoints in rats responding on progressive-ratio schedules for the opportunity to run for 60 s. Breakpoints for rats were higher after food restriction to establish a 75% body-weight level than after free feeding to maintain 100% of ad-libitum body weight. Wheel-running rates were also higher in 7 of 9 rats after reduction in food consumption to establish low body weight.

Together these studies indicate that restriction of food consumption, and the accompanying weight loss, increases the baseline rate of wheel running relative to lever pressing. When a schedule of reinforcement requires instrumental lever pressing for contingent wheel running, the wheel activity is constrained far below baseline, and contingent wheel running functions as reinforcement for operant or instrumental lever pressing. For the current study involving a multiple schedule, we expected that experimentally imposed food restriction would increase wheel-running and lever-pressing rates and decrease PRP duration in the component where lever pressing produced contingent wheel running.

Sucrose consumption (Pecoraro, Gomez, Laugero, & Dallman, 2002) and operant responding for sucrose reinforcement (Belke, 2004) also vary with feeding regime and body weight level. Pecoraro et al. (2002) showed that rats deprived of food to 85% of ad-lib weight consumed twice as much sucrose solution as did free-feeding rats at ad-lib weight. Belke (2004) showed that responding in the presence of a stimulus signaling sucrose on a fixed-interval (FI) schedule was reduced with a change in food allocation that led to a high body-weight level. Thus, as was the case for wheel running, restriction of food consumption and loss of body weight were expected to increase the baseline level of sucrose consumption relative to lever pressing, increase the constraint on drinking sucrose within a reinforcement schedule and lead to higher rates of instrumental lever pressing for contingent drinking of sucrose.

Currently, the effects of food restriction on instrumental wheel running for contingent intake of sucrose have yet to be investigated. Prior research, however, indicates that drinking sucrose does reinforce instrumental wheel running after rats have been food restricted and are at low body weight (Belke & Pierce, 2015; Belke et al., 2015). These findings suggest that, although food restriction increases the baselines for both sucrose consumption and wheel running, contingent drinking of sucrose remains the more restricted behavior; thus, drinking sucrose should reinforce wheel running in the operant component of the multiple schedule.

We also expected that under free-feeding conditions and ad-lib body weight, wheel running would no longer assume a food-related function, but rats would continue to run in wheels based on the intrinsic motivation of this activity (Belke & Pierce, 2016). Within a behavior system approach, wheel running is usually analyzed as general locomotion related to food search and procurement (Timberlake, 2001). That is, the function of wheel running in the natural ecology of rodents is viewed as general search behavior motivated by response deprivation (low food consumption) imposed by food restriction, increasing the likelihood of contact with a variable or intermittent food source. Our previous research, however, shows that rats run in their wheels at high levels even under free-feeding conditions, indicating that wheel running, unconstrained by a contingency, is behavior with a high probability baseline (Belke & Pierce, 2016). In addition, previous research on multiple