Automatic reinforcement from operant wheel-running undermines temporal control by fixed-interval schedules of reinforcement

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ABSTRACT

The current study compared the development of response patterns for operant wheel-running and lever-pressing on fixed-interval schedules. Eleven female Long-Evans rats were exposed to fixed-interval (FI) 15-s, 30-s, and 60-s schedules with wheel revolutions as the operant behavior and sucrose solution as reinforcement. Subsequently, a lever was mounted in each wheel and rats responded on an FI-30 s schedule of sucrose reinforcement. Operant lever-pressing on average developed a scalloping pattern of low responding early in the reinforcement interval followed by an increase in pressing to the moment of reinforcement. In contrast, average operant wheel-revolutions peaked early in the reinforcement interval followed by a plateau, a pattern that did not change over sessions. Variation in the FI-schedule value (interval size) with operant wheel-running did not alter the pattern of running throughout the reinforcement interval, but merely parsed this pattern at different points. Cumulative records for the last session showed long postreinforcement pauses (PRP) for lever pressing. Wheel running, however, rose quickly after reinforcement and continued throughout the reinforcement interval. Overall and local wheel-running rates decreased and PRP duration increased as the interval size of the FI schedule increased. We propose that the automatic reinforcement generated by wheel running, but not lever pressing, provides an account of the poor temporal regulation of operant wheel-running in our study.

1. Introduction

Running in a wheel is a behavior that can function as both a reinforcing consequence for an operant behavior such as lever pressing and as an operant behavior producing contingent reinforcement. While the reinforcement function of wheel running has been studied extensively (e.g., Belke, 1996, 1997, 2000, 2004, 2007; Belke and Hancock, 2003; Belke and Pierce, 2016; Belke et al., 2004; Belke and Wagner, 2005; Collier and Hirsch, 1971; Iversen, 1993; Kagan and Berkun, 1954), there have been few investigations of wheel running as an operant (Belke and Pierce, 2015; Belke et al., 2017; Iso, 1996; Premack and Tapp, 1969; Skinner and Morse, 1958). The operant function is of particular interest in the present study, as operant wheel-running results in experimentally arranged reinforcement for behavior that is itself reinforcing. That is, wheel running generates automatic reinforcement, emanating from engaging in the behavior itself, not from the experimental contingencies (Skinner, 1953, 1957; Vaughan and Michael, 1982). Although automatic reinforcement is sometimes used synonymously with concepts such as "intrinsic motivation" or "intrinsic reinforcement", the concept of automatic reinforcement allows for the possibility of behavior generating consequences just by doing it, regardless of location (intrinsic or extrinsic).

Rats run in their wheels based on the automatic reinforcement that follows from engaging in wheel running—plausibly emanating from the sensory feedback of the activity (sight, sound, and kinesthetic feedback of the wheel)(Weasner et al., 1960), from the upward angular momentum and speed of self-generated wheel activity (Sherwin, 1998), something akin to the fun and thrill of going on a roller coaster as a child, or from physiological changes in neural centers of the brain associated with reinforcement (Monroe et al., 2014).

Research relevant to this concept of automatic reinforcement has shown that although wheel running has a higher operant level than a conventional operant such as lever pressing, it can be reinforced by delivery of contingent sucrose solution. The magnitude of the strengthening effect is modest relative to that observed with lever pressing (Belke and Pierce, 2015; Belke et al., 2017, 2015), but varies with the sucrose concentration (Belke et al., 2017). Removal of sucrose reinforcement (extinction) by replacing it with water reduces the rate of operant wheel-running, though only by 25%; in comparison the same change reduces lever pressing by 90% (Belke et al., 2015). Furthermore,

the strengthening effect of programmed sucrose reinforcement appears to be additive with the automatic reinforcement generated by wheel running (Belke and Pierce, 2015). Importantly, we have shown that the automatic reinforcement generated by wheel running occurs regardless of whether wheel running functions as reinforcement or as an operant (Belke and Pierce, 2015). Also, prior wheel running provided before experimental sessions diminishes the efficacy of wheel running as reinforcement (Belke, 2006; Skinner and Morse, 1958), and withholding the opportunity to run increases the reinforcing efficacy of wheel running (Belke and Heyman, 1994).

The present study was designed to extend our investigations of the automatic reinforcement properties of wheel running to fixed interval (FI) schedules of reinforcement—a schedule in which the first response after a fixed time is reinforced. Specifically, we expected that the automatic reinforcement generated by wheel running would serve as an alternative source of reinforcement for operant wheel-running on FI schedules of sucrose reinforcement. With a conventional operant behavior such as lever pressing, this programmed reinforcement is the only source of reinforcement and the periodicity of the delivery of this reinforcement leads to patterns of responding such as "scalloping" on longer FI schedules or "break-and- run" on shorter FI schedules (Staddon and Cerutti, 2003). One implication of automatic reinforcement, as a competing source of control over responding on FI schedules, is that operant wheel-running would itself generate consequences, which would disrupt or interfere with the development of temporal control exerted by the programmed FI schedule of sucrose reinforcement.

The "scallop" describes a response pattern in which the animal pauses after reinforcement, response rate accelerates throughout the reinforcement interval, and maximal rate of response occurs at the moment of reinforcement— producing a convex curve traced in real time on a cumulative record. "Break-and-run", on the other hand, describes a response pattern in which the animal pauses following reinforcement then abruptly switches to a high steady rate of responding to the moment of reinforcement – yielding a stair-step pattern on a cumulative record. Both patterns have been observed in cumulative records for individual reinforcement intervals (Dews, 1978; Ferster and Skinner, 1957; Schneider, 1969) and both are indicative of temporal regulation of responding; however, when these response patterns are averaged across reinforcement intervals, a scalloping pattern is more likely to emerge (Baron and Leinenweber, 1994; Schneider, 1969).

Both scalloping and break-and-run response patterns have been demonstrated on FI schedules with numerous species, including rats (Baron and Leinenweber, 1994, 1995; Lowe and Harzem, 1977), pigeons (Berry et al., 2012; Lowe and Harzem, 1977; Schneider, 1969), monkeys (Dews, 1978), hamsters (Anderson and Shettleworth, 1977), woodmice (Lejeune and Wearden, 1991), prairie dogs (Todd and Cogan, 1978), bats (Beecher, 1971), crows (Powell, 1972), and fish (Higa and Simm, 2004; Talton et al., 1999) as well as with a variety of responses including lever pressing (Baron and Leinenweber, 1994, 1995; Dews, 1978; Lowe et al., 1979), key pecking (Gentry et al., 1983; Lowe et al., 1979; Schneider, 1969), nose poking (Blough, 1980; Fish et al., 2002), head pressing, and treadle pressing (Lejeune and Wearden, 1991).

Comparative studies, on the other hand, have shown that the development of these patterns varies across species (Lejeune and Wearden, 1991) and with characteristics of the operant (Richelle and Lejeune, 1980). With respect to the operant, it is notable that temporal regulation of behavior can vary with degree of similarity between the operant and consummatory responses. Thus, treadle pressing shows better temporal control than key pecking (Hemmes, 1975). And, Richelle and Lejeune (1980) concluded that "in tasks involving temporal regulation, the type of performance also depends upon the selected operant" (p. 121).

With respect to wheel running, only two studies have investigated wheel running as an operant on FI schedules of reinforcement. Skinner

and Morse (1958) used two brown rats and arranged a FI 5-min schedule, which was preceded and followed by 30-min access to a freely turning wheel. Food pellets were delivered as reinforcement for operant wheel-running and the operation of the FI schedule was signaled by a 6-watt light. The FI schedule remained in effect until a fixed number of reinforcements were completed (initially 50, then 40, then 20 reinforcements). Cumulative records showed evidence of typical FI patterns of a postreinforcement pause (PRP) followed by an acceleration of running, but with an unexpected deceleration in running just prior to reinforcement. Skinner and Morse attributed the deceleration to the animals investigating the food magazine as the moment to reinforcement approached, although they did not present data of such exploratory behavior. Notably, the rate of wheel running on the FI schedule was higher than the preceding and following free-running periods, but freely available wheel running showed a high operant level even without any programmed contingencies of reinforcement.

In a subsequent study by Iso (1996), three male Wistar rats were maintained at 74.7% of initial weight (high motivation to run) and required to run for 45-mg food pellets on a FI 60-s schedule of reinforcement with the operant defined as a quarter turn, rather than a complete revolution, of the running wheel. The pattern of responding on the FI 60-s schedule was compared to three other male Wistar rats on a yoked FI 60-s schedule. After six training sessions, the rats on the FI 60-s schedule completed another 10 sessions as did the yoked-control animals. Iso noted that one animal with the lowest rate on the FI 60-s schedule showed scalloping in the cumulative record. For rats in the yoked-control group, on the other hand, wheel running began shortly after reinforcement then, following a bout of responses, paused for the rest of the reinforcement interval—a pattern consistent with adjunctive behavior (Falk, 1961, 1969; Wetherington, 1982). In a second experiment, four rats were trained on a FI 30-s schedule and then switched to a FI 60-s schedule of reinforcement for 10 sessions. In this experiment, rats were maintained at 91% of ad-lib weight to reduce motivation for wheel running. In this case, Iso found scalloping in the cumulative records of each of the four rats. Thus, scalloping developed more consistently when motivation for wheel running was lower (91% vs. 75% of initial body weight). Finally, in extinction sessions conducted in both studies, Iso reported that rats continued to run on wheels at high rates even when food reinforcement was no longer available. Importantly with respect to the concept of automatic reinforcement, Iso concluded that "there might have been some other reinforcing stimuli than food reinforcement in this wheel-running procedure" (Iso, 1996, p. 58). In sum, both Skinner and Morse (1958) and Iso (1996), using different procedures, concluded that operant wheel-running can show response patterns consistent with temporal regulation of responding.

A second objective of the present study concerns the effect of reinforcement interval on pausing and response rates of operant wheel-running on FI schedules. Prior studies of lever pressing on FI schedules have shown that as the reinforcement interval increases, PRP duration increases (Lowe and Harzem, 1977; Lowe et al., 1979; Schneider, 1969; Shull, 1971; Zeiler and Powell, 1994) while overall and local response rates decrease (Lowe et al., 1979; Schneider, 1969). For example, Lowe et al. (1979) placed four rats on FI 15, 30, 60, 120, 240, and 480-s schedules with 45 mg food pellets as reinforcement. Results showed that as schedule value increased, PRP duration increased, while local and overall lever-pressing rates decreased. Furthermore, PRP duration is typically considered to be proportional to the duration of the reinforcement interval (Dukich and Lee, 1973; Nevin, 1973). Previous studies (Schneider, 1969; Shull, 1971) found that average PRP with pigeons pecking a key was approximately one half to two thirds of the reinforcement interval. With rats, Lowe et al. (1979) found that PRP duration was not a constant percentage of FI schedule value, but decreased over FI schedules ranging from 15 s to 480 s. Regardless, presently there are no studies of average PRP or response rates for operant wheel-running on FI schedules of reinforcement.

In the current study, eleven female Long Evans rats were exposed to