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Research report

Dynamic behavioural changes in the Spontaneously Hyperactive Rat: 3. Control by reinforcer rate changes and predictability

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ABSTRACT

Variable intervals are widely believed to produce steady rates of responding. However, based on the calming effect of unpredictability in attention deficit hyperactivity disorder (ADHD) we hypothesised that an animal model of this disorder, the Spontaneously Hyperactive (or Hypertensive) Rat, would become less active following particularly variable sequences of interval-lengths in a variable interval schedule. From a large dataset of holepokes and tray-reports by rats in a variable interval reinforcement schedule, we extracted numerous short sequences of intervals on the basis of the first, second, and third derivatives of reinforcement timing (i.e. rate, acceleration, and jerk) in recent intervals. Sets of selected intervals were compared with one another to elucidate the effect of these different derivatives on behaviour in the current interval. Results show that SHR are more active after richer recent reinforcement; after decelerating reinforcers; and after predictable reinforcers. The hypothesis is supported. In conclusion, SHR behaviour largely complies with the Extended Temporal Difference model which in turn has been previously validated against published data in ADHD. The Extended TD model therefore is able to account for two species' behaviour in a wide range of experimental paradigms. SHR are similar in several respects to group averages of children with ADHD, except that SHR have reduced variability and perform actions faster than controls. Hyperactivity in the SHR is very dependent on momentary environmentally determined states, which is an important area for future investigation of ADHD.

1. Introduction

We have previously shown that an increased drive for novelty or sensation-seeking, with their conjoined partner of low anxiety, explains much of the SHRs' extremely high rate of holepoking and its spatial and temporal specificity [25,28]. However, the current paper attempts to measure components of these factors more quantitatively.

This paper focusses on a timescale of seconds to minutes, both for data analytic reasons and because clear *changes* in SHR behaviour have been identified that occur over time-scales shorter than a single session [28]. The aim here is to analyse the determinants of hyperactivity in the SHR, in order to develop hypotheses for the aetiology of ADHD. Specifically, this study tests the hypothesis that inter-strain differences can be found in behavioural responses to changes in reinforcer timing over the timescale of a few intervals (approximately 1–5 min).

2. Background

What are the potentially rewarding (novel or intriguing or pleasant) aspects of holepoking? The great majority of holepokes are unrewarded, in which case they actually provide considerably less sensory input than the water-tray, which has a cover that has to be pushed aside, and a dipper behind it. At sufficiently long delays after the last reinforcer delivery, reinforcement becomes inevitable so that an ideal learner could not be surprised by it. The bang itself is not novel to the rats, though the juxtaposition between a non-banging holepoke and a banging one may be quite intriguing. Alternatively (or additionally), the rat may have been steadily holepoking for a whole minute without reward, each time adjusting downwards his estimate of the likelihood of reward. So the longer he had waited, the lower his estimate would be, and the greater his

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pleasant surprise. The rat might like (or hate) the unpredictability of variable intervals, or might be constantly hoping for a happy moment when the drips start coming much faster. The list could continue.

If an engineer were designing a robot to predict the time of the next reward, he would probably base it on the rate (the first derivative of the reward times). If the rate changed, he might base his prediction on a running average, or on a trend such as the acceleration or deceleration (second derivative) of the rewards. He might even use the third derivative (jerk) to try to make better predictions.

This paper can be viewed as an attempt to reverse-engineer the rats in the holebox VI dataset in this way, based on the assumption that the engineer's principles are so efficient that they may have been influential during the evolution of rats.

3. Method

The dataset has been described in detail previously [25,28]. The approach taken here is somewhat more complicated than those studies, in which all the rats' actions during a particular time period were binned in various ways, and shown in what was essentially time order. Here programs are used to find the subset of intervals that satisfy a particular criterion, and then these are compared with other subsets fitting related criteria.

4. Results

In order to shed more light on the local or proximate trigger for SHR hyperactivity, effects of increasing and decreasing reinforcer densities were analysed. For this purpose, analysis focussed on intervals that *followed* triplets of intervals that showed a clear trend. These intervals were further subdivided according to the second-back interval (b in Fig. 1) so the resulting figure shows the effect of both rate and acceleration (of reinforcers) on holepoking rate (Fig. 1). Tightening the restriction on interval selection, so preceding interval lengths a,b, and c all had to be in the time range, gave similar results but with smaller sample size (result not shown).

The results show that SHR holepoking is greatest when recent reinforcers have been slowly decelerating (in the figure, x from 1.0 to 1.5), yet overall recent reinforcer rate had been greater than the schedule mean (see Fig. 1(A) and (B)). There were smaller differences between SHR and WKY response output when inter-reinforcer time had recently decreased, i.e. when local reinforcer density had increased (extreme left of Fig. 1(A)–(C)).

Relationships between the rate of holepoking and the variability of the two previous IRfTs were analysed. Results show that the coefficient of variation of recent IRfTs is an important predictor of the holepoking rate of SHR, but not WKY (Fig. 2(B)). This will be discussed below.

A classical explanation for this effect would be that greater IRfT variability was associated with a *lower* density of reinforcers, thus causing a reduction in response rate. This possibility was examined by looking at the relationship between the IRfTs in recent intervals, and the response rate (Fig. 2(C)). This showed that the mean of the two most recent IRfTs predicts very little of the variability in mean response rate, though the error-bars show that the most of what it fails to capture is in relatively short IRfT means. The immediately preceding IRfT did have an effect on holepoking (Fig. 2(D)), but in the opposite direction to that predicted by the classical explanation: Following short IRfTs, SHRs have a slight tendency to holepoke *less* often, and to be more similar to the WKYs.

The above analyses have shown that the recent reinforcer history (including timing, density, variability, and acceleration) is more important for determining response output in SHRs than in WKYs. In order to shed light on the relative importance of reinforcer prediction, versus unpredictability per se, in the control of SHR

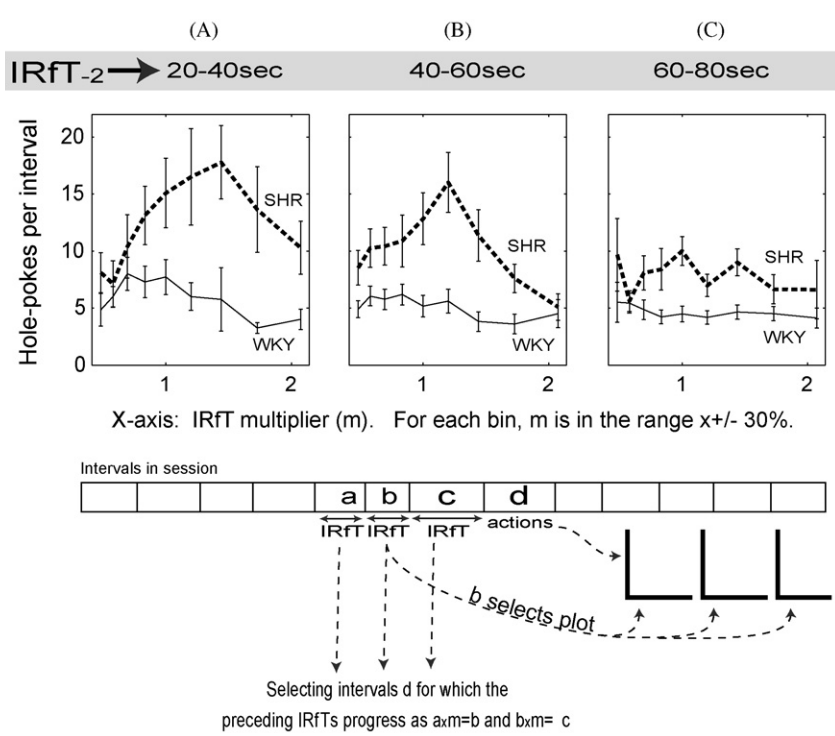

Fig. 1. Effect of trend of recent inter-reinforcer interval, on holepoking, by recent inter-reinforcer density. Responses are shown for intervals in which the lengths of the second previous IRfT (shown as b in the lower diagram) were very short, somewhat short, or somewhat long (A, B, or C respectively), in comparison with the overall reinforcement schedule. The x-value of each point is a measure of the lengthening trend, or IRfT multiplier (m) of a, b, c: 1 = stable; <1 = shortening; >1 = lengthening. The y-value of each point is the mean number of holepokes made in interval "d". Error-bars are S.E.M., based on the number of intervals. Durations shown are approximations: 1 s = 18.2 time units, recalculated as 20 t.u. for readability.