Behavioural Brain Research 271 (2014) 184–194

Contents lists available at ScienceDirect

Behavioural Brain Research

journal homepage: www.elsevier.com/locate/bbr

Research report

Different relations between schedule-induced polydipsia and impulsive behaviour in the Spontaneously Hypertensive Rat and in high impulsive Wistar rats: Questioning the role of impulsivity in adjunctive behaviour

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HIGHLIGHTS

- The SHR showed higher prior impulsivity than WKY controls in delay discounting.
- SHRs showed higher adjunctive drinking at long inter-food intervals than WKY rats.
- High- vs. low-impulsive Wistar rats showed in general less schedule-induced drinking.
- Retesting delay discounting resulted in a convergence among the groups of rats.
- Impulsivity is not an adequate predictor of schedule-induced polydipsia development.

ARTICLE INFO

Article history:
Received 22 December 2013
Received in revised form 3 June 2014
Accepted 6 June 2014
Available online 13 June 2014

Keywords:
Schedule-induced polydipsia
Delay discounting
Indifference point
Excessive behaviour
SHR
Wistar rats

ABSTRACT

Rats belonging to three different strains (15 Wistar, 8 Spontaneously Hypertensive – SHR- and 8 Wistar Kyoto – WKY-) were used to evaluate the possible relationship between different levels of impulsivity and development of schedule-induced polydipsia (SIP). We first measured the rats' levels of impulsivity by means of delay-discounting and indifference-point procedures. Secondly, development of SIP was studied under a series of fixed time 15, 30, 60 and 120 s food schedules, which were counterbalanced by means of a Latin-square design. Finally, we re-assessed the rats' levels of impulsivity by replicating the delay-discounting test. The findings showed that, starting from equivalent levels of impulsivity, development of SIP differed among the groups of rats. In comparison with the rest of the animals, the SHRs were observed to attain elevated drinking rates under SIP. On the other hand, the Wistar rats which had initial high impulsivity levels similar to those of the SHRs, displayed the lowest rates of induced drinking. Moreover, low levels of impulsivity in Wistar rats prior to SIP acquisition were reflected into high drinking rates. Relation of SIP and impulsivity is questioned by present results, which gives ground to the understanding of the behavioural mechanisms involved in adjunctive behaviour and its usefulness as an animal model of excessive behaviour.

1. Introduction

Falk [17] observed that, if rats were allowed free access to a water bottle under intermittent food-delivery conditions, they developed a characteristic drinking pattern in the inter-food intervals, i.e., the animals drank a small quantity of water after each food episode, with this drinking becoming excessive across the experimental session, as a result of repetition in the administration of food and prolonged experience of the reinforcement schedule [17,18] (for demonstrations of the phenomenon in our laboratory, see [21,23,42]). Falk termed such excessive consumption of water, "schedule-induced polydipsia" (SIP) (since neither physiological- nor behavioural-regulation mechanisms could account for it), with this being proposed as a model of the class of behaviour known as interim [51] or adjunctive [19].

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http://dx.doi.org/10.1016/j.bbr.2014.06.010
0166-4328/

Although other types of adjunctive behaviour have been observed, such as wheel-running in rats [31] and induced attack in pigeons [32], SIP has become the prototype of animal models of adjunctive behaviour, having received the largest share of behavioural [29,40,41] and neuropharmacological research [24,37].

Polydipsic drinking has been induced in rats as a model of behavioural excess, and attempts have been made to link this behaviour to different disorders in which impulse control fails or the behaviour intensifies for no apparent reason [45]. SIP has likewise been proposed as a model of addiction [13] and obsessive disorder [46,54,60]. Several pharmacological studies have also evaluated differences in SIP in relation to different levels of impulsivity [10,11].

Impulsive behaviour mainly comprises deficit in inhibitory control, precipitate decision-making, hypersensitivity to delay in reward and short attention span [15], which has led impulsivity to be divided in two different types: on the one hand "motor impulsivity", in which behavioural excess is mainly to blame for the consequences, and on the other "cognitive impulsivity", which entails precipitate decision-making that tends to lead to undesired consequences for the individual [8,15]. Impulsive responses, however, will in most cases have a motor and a cognitive component. High levels of impulsivity rise to an extreme in several psychiatric disorders such as mania, substance abuse or attention-deficit/hyperactivity disorder (AD/HD).

Impulsivity levels can be assessed prior to any other experimental procedure to obtain a measure of trait impulsivity [28,44] that, in turn, can be used as a vulnerability marker to diseases where impulse control fails, like drug dependence [7,34].

The Spontaneously Hypertensive Rat (SHR) [39,53] has traits such as hyperactivity, inattention and elevated sensitivity to delay in the reinforcer, aspects that tend to come together in impulsive behaviour [57,61]. This has led to this animal being validated as a model of AD/HD, a disorder in which impulsivity plays a principal role [4,5,14,30,35,47]. Within the AD/HD spectrum, SHRs fit into the hyperactive subtype in particular [2,3,48,52]. In comparison with its normotensive Wistar Kyoto (WKY) control [20,50,56], the SHR exhibits impulsivity [25,49].

SHRs' hypersensitivity to delay in the reinforcer becomes manifest on their being required to wait before emitting the response sequence to the behavioural criterion, whether by training in low response rates or the introduction of a delay in order to obtain the reinforcer [16]. In such self-control situations, SHRs display inattention and impulsivity. Due to their hyperactivity, these animals' behaviour turns principally on behavioural excess which, in one way or another, eventually manifests itself as impulsive behaviour.

While behavioural excess poses a problem when it comes to inhibiting, extinguishing or reinforcing conditioned behaviour at low rates, this selfsame excess might, on the other hand, promote faster learning of other behaviours. Williams et al. [57] put this hypothesis to the test by studying the ability of SHRs to modify their behaviour (entering an opening in a panel to obtain water) during a Variable Interval (VI) 60-s reinforcement schedule, with reference to the duration of the immediately preceding trials. SHRs proved more capable of increasing or decreasing their behaviour in a matter of minutes than did the WKY rats, but they nevertheless did not seem capable of reducing their behaviour permanently over a period of weeks. Furthermore, these rats tended to make excessive use of the most recent information in preference to other longer-term information [57,58].

Other evidence of excessiveness in SHRs is to be seen in a slower extinction of behaviours such as lever pressing [6]. This has been shown when compared to WKY rats after Fixed Interval (FI) and VI reinforcement schedules, with more unreinforced responses (because of the extinction procedure) both in the presence and in the absence of predictive cues of cancellation of the reinforcer [27].

We [26] have investigated SIP performance of SHRs after exposing the animals to a counterbalanced series of Fixed Time (FT) food schedules (of 9, 15, 30, 60, 120 and 180 seconds) with water available throughout the inter-food intervals in order to generate different levels of drinking as a function of food frequency, and differences were reported in the sense of, mainly higher drinking levels among the SHRs under FT schedules with longer inter-food intervals, and higher rates among the Wistar rats under shorter schedules. Once this procedure was completed, animals were trained in self-control using a delay-discounting test [1,25,33,59], being found that SHRs made more impulsive decisions and committed more omissions with delays of 12 and 24 s to obtain the larger but delayed reward.

The present study follows on from some of the questions that arose out of the previous one [26]. To what extent the SHRs' impulsivity, mediated by their behavioural excess in SIP performance, is transferable to other impulsive but not necessarily hyperactive, subjects. Therefore, it would be of interest to take a control population of Wistar rats and, after screening two groups according to their measures of impulsivity, ascertain to what extent they would share the traits of impulsivity and self-control shown by SHRs and WKY rats. Moreover, it would be also interesting to study how sensitivity to the delayed reinforcer develops as a sign of impulsivity as the result of repeated experience with the same delayed reinforcer. Firstly, we measured the levels of impulsivity displayed by the rats, along with value assigned by them to delay under impulsivity test conditions. Secondly, we implemented a SIP procedure using FT schedules with different inter-food interval values counterbalanced by means of a Latin-square design. Thirdly, we reassessed the rats' impulsivity levels by replicating the delay-discounting test. Apart from the delay-discounting task, prior to the SIP-based experience, an indifference-point test was conducted. The animals were given the opportunity of choosing between a large delayed reward and another smaller immediate reward under conditions that favoured the choice of the large delayed reward: subsequently, the magnitude of the immediate reward was varied, until there was a shift in preference away from the delayed reward towards the immediate reward. The magnitude of the immediate reward would indicate the value assigned to the delay, which should logically be smaller in SHRs than in WKY rats, and which might also depend on the Wistar rats' level of impulsivity.

2. Methods

2.1. Subjects

We used 32 male rats belonging to three different strains -8 SHR, 8 WKY and 16 Wistar- obtained from the Charles River Laboratories (Lyon, France). On arrival at the laboratory they were 10 weeks old. They were housed for 15 days in groups of four in an environmentally-controlled room with a 12-h light-dark cycle (light from 08:00 to 20:00 h), an ambient temperature of 21 °C and 65% relative humidity. Once habituated to the animal facility, the rats were housed singly in 18 × 32.5 × 20.5 cm transparent Plexiglas cages with a metal grid detachable roof that enabled food to be deposited and a water bottle to be fitted, and were kept there without any type of experimental manipulation for 10 days.

At the end of the adaptation period, the animals' mean weight was as follows: 278.12 g (range 266–288 g) in the case of SHRs; 339.12 g (range 302–358 g) in the case of WKY rats; and 339.21 g (range 318–373 g) in the case of Wistar rats. Using a controlled diet, animals were reduced to 82–85% of their free-feeding weight, which was then maintained throughout the experiments in proportion to the weight established by standard growth curves for each strain. Each rat was manipulated and weighed daily before each