Behavioural Processes 87 (2011) 18–24

Contents lists available at ScienceDirect

Behavioural Processes

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

Nicotine and the behavioral mechanisms of intertemporal choice

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ARTICLE INFO

Article history:
Received 15 September 2010
Received in revised form 16 February 2011
Accepted 16 February 2011

Keywords:
Nicotine
Rats
Intertemporal Choice
Impulsive choice
Variable interval
Concurrent chains

ABSTRACT

Nicotine has been found to produce dose-dependent increases in impulsive choice (preference for smaller, sooner reinforcers relative to larger, later reinforcers) in rats. Such increases could be produced by either of two behavioral mechanisms: (1) an increase in delay discounting (i.e., exacerbating the impact of differences in reinforcer delays) which would increase the value of a sooner reinforcer relative to a later one, or (2) a decrease in magnitude sensitivity (i.e., diminishing the impact of differences in reinforcer magnitudes) which would increase the value of a smaller reinforcer relative to a larger one. To isolate which of these two behavioral mechanisms was likely responsible for nicotine's effect on impulsive choice, we manipulated reinforcer delay and magnitude using a concurrent, variable interval (VI 30 s, VI 30 s) schedule of reinforcement with 2 groups of Long–Evans rats ($n = 6$ per group). For one group, choices were made between a 1-s delay and a 9-s delay to 2 food pellets. For a second group, choices were made between 1 pellet and 3 pellets. Nicotine (vehicle, 0.03, 0.1, 0.3, 0.56 and 0.74 mg/kg) produced dose-dependent decreases in preference for large versus small magnitude reinforcers and had no consistent effect on preference for short versus long delays. This suggests that nicotine decreases sensitivity to reinforcer magnitude.

1. Introduction

An intertemporal choice is a choice between two or more alternatives that differ in reinforcer magnitude, reinforcer delay, or both reinforcer magnitude and delay (Loewenstein and Elster, 1992). Perhaps the most commonly studied intertemporal choices are impulsive choices: choices for a smaller-sooner reinforcer over a larger-later reinforcer (for review see Frederick et al., 2002). Anecdotal evidence for a relationship between nicotine and impulsive choice has been accumulating for many years. In 1952 Reader's Digest published "Cancer by the Carton", a public alert to the health dangers of smoking. About 15 years later, every package of cigarettes sold in the United States was required to prominently display a health warning. As knowledge of the health benefits of smoking abstinence spread, so too did the prevalence of smoking. Millions of people, on a daily basis, seemed to be choosing a smaller-sooner reinforcer (an immediate cigarette) over a larger-later reinforcer: delayed health benefits.

Bickel et al. (1999) used a delay-discounting task to compare impulsive choices made by smokers, non-smokers, and ex-smokers. In this task, human participants made choices between $1000 after a delay versus some amount of money to be delivered immediately (all consequences were hypothetical). By adjusting the immediate amount of money, Bickel et al. determined the immediate amount of money that was equally preferred to $1000 after a particular delay, a so-called indifference point. This process was repeated using six other delays ranging from 1 week to 25 years, thus yielding seven indifference points. Mazur's (1987) hyperbolic discounting equation was fitted to the data:

$$V = \frac{M}{1 + kD}, \tag{1}$$

where V represents the current value of a delayed reinforcer, M represents the reinforcer magnitude[1] (in USD, in this case), D represents the delay to the reinforcer, and k is a free parameter which reflects the rate at which the reinforcer loses value with increases in delay – thus k indicates the degree of delay discounting.

[1] Mazur's original (1987) equation used A for reinforcer amount rather than M for reinforcer magnitude. Reinforcer magnitude is used in Eq. (1) as it is more generally applicable (e.g., to choices between a whole candy bar and a piece of a candy bar). Similarly, a nicotine effect on magnitude sensitivity might be more plausible than an effect on amount sensitivity. For example, nicotine enhancing the value of small reinforcers seems more likely than nicotine enhancing the value of low-quantity reinforcers. However, the only magnitude manipulation in the current experiment was accomplished by manipulating amount (number of homogenous food pellets), and so whether amount or magnitude is more appropriate in this particular context remains an unanswered empirical question.

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doi:10.1016/j.beproc.2011.02.006

Bickel et al. (1999) found a median k for smokers of 0.054. The degree of discounting for both never-smokers (those who reported to have never smoked a single cigarette) and ex-smokers (those who reported to have smoked previously but abstained for at least 1 year) was identical: 0.007. This correlation between smoking and impulsive choice suggests that either impulsive people are more likely to smoke (and not quit), or that nicotine increases impulsive choice. Dallery and Locey (2005) addressed this issue by examining the effects of acute and chronic nicotine administration on choice in an impulsive-choice procedure with rats. The logic of the impulsive-choice procedure was similar to the human delay-discounting task, with rats making repeated choices between a single food pellet delayed 1 s and 3 food pellets after an adjusting delay. Once an indifference delay was determined for each rat, nicotine was administered to each rat 10 min prior to the behavioral task. Dallery and Locey found a dose-dependent increase in impulsive choice for all rats. Although this finding does not eliminate the possibility that more impulsive people are more likely to smoke, it does suggest that those who smoke may become more impulsive as a direct result of the nicotine.

Eq. (1) has also proven effective in describing and predicting risky choice (Mazur, 1984). A risky choice is a choice for a more variable rate of reinforcement over a less variable rate of reinforcement (Bateson and Kacelnik, 1995; McNamara and Houston, 1992). If nicotine increases delay discounting (k), then it should increase preference for a variable delay over a fixed delay just as it increases preference for a smaller-sooner reinforcer over a larger-later reinforcer. Locey and Dallery (2009) found no such increases in risky choice, in rats, comparing an adjusting delay to a variable delay of 1 s ($p = .5$) and 19 s ($p = .5$). In this initial experiment, a single food pellet was arranged for both alternatives. Locey and Dallery (2009) next replicated the risky-choice experiment but introduced different reinforcer magnitudes: finding the adjusting delay to 3 pellets that was equally preferred to 1 pellet delayed either 1 s or 19 s. With this one change in the procedure, nicotine showed a dose-dependent increase in risky choice very similar to the change observed in Dallery and Locey (2005) impulsive-choice procedure. These findings suggest that nicotine only affects intertemporal choice when the choice alternatives differ in reinforcer magnitude.

The present experiment was designed to further explore what effects nicotine might have on these two behavioral mechanisms of intertemporal choice: delay sensitivity (or delay discounting[2]) and magnitude sensitivity. Previous attempts to disambiguate the effects of psychomotor stimulants on sensitivity to reinforcer magnitude and delay have met with mixed results. Pitts and Febbo (2004) found that amphetamine decreased sensitivity to reinforcer delay without impacting sensitivity to reinforcer magnitude. Roesch et al. (2007) found that cocaine increased sensitivity to both reinforcer magnitude and delay. da Costa Araújo et al. (2010) proposed likely separate neural mechanisms involved with changes in magnitude versus delay sensitivity.

In the present study, concurrent variable interval (VI) schedules of equal duration (30 s) were used to arrange choices between different delays to food in one group and different amounts of food in the other group. If nicotine decreases magnitude sensitivity but has no effect on delay sensitivity, this should be revealed by dose-dependent decreases in relative preference for the lever associated with the large amount of food (for the magnitude group) and no dose-dependent changes in relative preference for the short delay alternative (for the delay group).

2. Material and methods

2.1. Subjects

Twelve experimentally naïve Long–Evans hooded male rats (Harlan, Indianapolis, IN) were housed in separate cages under a 12:12 h light/dark cycle with continuous access to water. Each rat was maintained at 85% of its free-feeding weight as determined at postnatal day 150. Supplemental food was provided in each rat's home cage following each session. The weight of food supplements were calculated daily for each rat, using the difference between each rat's pre-session weight and its 85% weight.

2.2. Apparatus

Seven experimental chambers (30.5 cm L × 24 cm W × 29 cm H) in sound-attenuating boxes were used. Each chamber had two (2 cm L × 4.5 cm W) non-retractable levers 7 cm from the chamber floor. Each lever required a force of approximately 0.30 N to register a response. A 5 cm × 5 cm × 3 cm food receptacle was located 3.5 cm from each of the two levers and 1.5 cm from the chamber floor. The food receptacle was connected to an automated pellet dispenser containing 45 mg Precision Noyes food pellets (Formula PJPPP). Three horizontally aligned lights (0.8 cm diameter), separated by 0.7 cm, were centered 7 cm above each lever. From left to right, the lights were colored red, yellow, and green. A ventilation fan within each chamber and white noise from an external speaker masked extraneous sounds. A 28 V yellow house light was mounted 1.5 cm from the ceiling on the wall opposite the intelligence panel. Med-PC™ hardware and software controlled data collection and experimental events.

2.3. Procedure

2.3.1. Training

Lever pressing was initially trained on a conjoint fixed-ratio (FR) 1, random-time (RT) 100-s schedule. The houselight was turned on for the duration of each training session. Training trials began with the onset of all three left-lever lights. In the initial trial, both levers were active so that a single response on either lever resulted in immediate delivery of 1 food pellet. The RT schedule was initiated at the beginning of each trial so that a single pellet was delivered, response-independently, approximately every 100 s. Both response-dependent and response-independent food deliveries were accompanied by the termination of all three lever lights. After a 2-s feeding period, the lights were illuminated and a new trial began. After two consecutive presses of one lever, that lever was deactivated until the other lever was pressed. After a total of 60 food deliveries, the session was terminated. Training sessions were conducted for 1 week, at the end of which all response rates were above 10 per minute.

2.3.2. Concurrent VI baseline

Rats were randomly assigned to either the magnitude ($n = 6$) or delay ($n = 6$) group. In the magnitude group, choices resulted in either 1 pellet (if the "small lever" was chosen) or 3 pellets (if the

[2] No distinction is made in the present manuscript between delay discounting and delay sensitivity. This is not to say that the two are identical. Mathematically, delay sensitivity has been defined as s in either of the following variations of Eq. (1):

$$V = \frac{M}{(1+kD)^s} \quad \text{(Rachlin, 1989)} \quad \text{or} \quad V = \frac{M}{1+kD^s} \quad \text{(Mazur, 1987)}.$$

Both delay discounting (k) and delay sensitivity (s) alter the impact of delay (D) on reinforcer value (V). The procedure used in the present experiment was designed to determine if nicotine alters the impact of magnitude or delay on value. Because only a single pair of delays (1 s vs. 9 s) was used, any effect observed in the delay group could be due to either an effect on delay discounting or an effect on delay sensitivity. As such, "delay sensitivity" is used in the present manuscript to ambiguously refer to delay sensitivity and/or delay discounting.