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Choice in a variable environment: Effects of *d*-amphetamine on sensitivity to reinforcement

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ABSTRACT

Four pigeons responded under a 7-component mixed schedule in which each component arranged a different left:right reinforcer ratio (27:1, 9:1, 3:1, 1:1, 1:3, 1:9, 1:27). Components were unsignaled, and the order within each session was randomly determined. After extensive exposure to these contingencies, effects of a range of doses of *d*-amphetamine (0.3–5.6 mg/kg) on estimates of sensitivity to reinforcement at several levels of analysis were assessed. Under non-drug conditions, the structure of choice was similar to that previously reported under this procedure. That is, responding adjusted within components to the reinforcer ratio in effect (i.e., sensitivity estimates were higher in the 2nd than in the 1st half of components), and individual reinforcers produced "preference pulses" (i.e., each food presentation produced an immediate, local, shift in preference toward the response that just produced food). Although there was a general tendency for *d*-amphetamine to reduce overall sensitivity to reinforcement, the size of this effect and its reliability varied across pigeons. Further analysis, however, revealed that intermediate *d*-amphetamine doses consistently reduced sensitivity immediately following reinforcer presentations; that is, these doses consistently attenuated preference pulses.

1. Introduction

Much of the recent study of drug effects on choice and decision making has been aimed at characterizing effects of drugs on "impulsive" choices under conditions in which subjects choose between a smaller, less delayed reinforcer (the impulsive choice) and a larger, more delayed one (the "self-control" choice) (see de Wit and Mitchell, 2010 for a review). Interestingly, compared to this literature, there are relatively few published studies investigating effects of drugs on choice controlled by relative reinforcement rate.

Todorov et al. (1972) exposed pigeons to multiple schedules with components consisting of different pairs of concurrent variable-interval (VI) schedules arranged via a Findley-switching procedure. *d*-Amphetamine produced dose-related decreases in rates of responding on both the switching key and the main key. Rates of switching, however, were decreased to a greater extent than were rates of responding on the main key.

Ziriax et al. (1993) examined effects of *d*-amphetamine in monkey's responding under concurrent stochastic-reinforcement-of-waiting (SRW) schedules. An SRW schedule is similar to a VI schedule, but reinforcement rate is less affected by response rate under an SRW than under a VI schedule. During baseline, relative time allocation matched relative reinforcement rate. *d*-Amphetamine decreased both overall response rates and switch rates, but the effects on time allocation were unsystematic. Microanalysis indicated that *d*-amphetamine produced longer inter-response times and longer visit durations on the richer SRW schedule. Ziriax et al. suggested that such microanalyses of behavior were necessary to elucidate behavioral mechanisms of drug action and to assess the validity of global measures of performance.

The studies described above involved examining drug effects on responding under steady-state conditions. There is growing interest, however, in studying choice dynamics under rapidly changing conditions. In some of these studies, reinforcement parameters change unpredictably across sessions (e.g., Grace et al., 2003; Kyonka and Grace, 2008; Hunter and Davison, 1985; Maguire et al., 2007); whereas in other studies, reinforcement parameters change unpredictably within sessions (e.g., Baum and Davison, 2004; Davison and Baum, 2000, 2002, 2003, 2007). After sufficient exposure to these procedures, behavioral allocation adjusts rapidly to the varying contingencies, although estimates of sensitivity to the manipulated reinforcer dimension(s) often are lower than those typically reported under steady-state conditions. Davison, Baum, and colleagues used several variants of a procedure originally described by Belke and Heyman (1994). Sessions consisted of seven components, each separated by a blackout. Each component was associated with a different reinforcer ratio (e.g., programmed reinforcer ratios on the left and right alternatives were 27:1, 9:1, 3:1, 1:1, 1:3, 1:9, and 1:27). Components were unsignaled and

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occurred in a random order. Several interesting, and potentially important, characteristics of choice were reported in this series of studies. For example, response allocation adjusted relatively rapidly within each component to the reinforcer ratio in effect for that component; sensitivity to reinforcement rate increased across successive reinforcers within a component. Local analyses revealed that each reinforcer delivery produced a "preference pulse," an immediate, and dramatic, increase in preference for the alternative that just produced the reinforcer. These preference pulses were transient in that they subsided with successive post-reinforcer responses.

Because each session, or each component within a session, arranges a different experimental condition, these types of procedures may provide effective baselines for the efficient study of drug effects on sensitivity to reinforcement parameters and, thus, may help us identify potential behavioral mechanisms of drug action. Furthermore, they also provide a set of tools to assess drug effects on the dynamics of behavior (i.e., behavior in transition).

TA et al. (2008) used a rapid-acquisition procedure to study effects of *d*-amphetamine on sensitivity to reinforcement delay. Delays to reinforcement associated with two terminal links of a concurrent-chains procedure varied unpredictably across sessions according to a pseudorandom binary sequence (PRBS; see Grace et al., 2003; Hunter and Davison, 1985). TA et al. found that *d*-amphetamine attenuated control by reinforcement delay (i.e., decreased sensitivity to delay) at doses that did not alter overall initial-link response rates. Furthermore, they found that, in general, *d*-amphetamine reduced the asymptotic level of preference achieved within a session, but had relatively little effect on the speed with which responding reached asymptote. In a few cases, however, *d*-amphetamine completely obliterated within-session acquisition of preference controlled by delay. Using a similar PRBS procedure, Maguire et al. (2009) reported that *d*-amphetamine decreased acquisition of preference controlled by reinforcer amount (i.e., *d*-amphetamine decreased sensitivity to reinforcer amount). Finally, Aparicio (2007) investigated effects of the dopamine antagonist haloperidol under the within-session procedure described by Davison, Baum, and colleagues. In Aparicio's study, reinforcer rate varied within components, while relative reinforcer amount varied across experimental phases. Haloperidol reduced overall rates of responding, but did not systematically affect the within-session acquisition of choice controlled by relative reinforcer rate; nor did it affect response allocation controlled by reinforcer amount.

The purpose of the present study was to characterize drug effects on the structure of choice within a variable environment. We used the basic procedure described by Belke and Heyman (1994) and Davison and Baum (2000) to investigate effects of *d*-amphetamine on choice controlled by relative reinforcement rate. Within each session, seven components, each programming a different left:right reinforcer ratio (ranging from 1:27 to 27:1) were arranged in the context of a mixed schedule (i.e., components were unsignaled).

2. Method

2.1. Subjects

Four Racing Homer pigeons (*Columba livia*) served as subjects. The pigeons had previous experience responding under the procedure described here (Rodewald et al., in press), but had not received drugs before the current study. Pigeons were maintained at 85% of their free-feeding weight via post session feeding (Purina Pigeon Checkers) and were housed individually in a colony room (12:12 h light:dark cycle) with free access to health grit and water.

2.2. Apparatus

Experiments were conducted in four identical operant-conditioning chambers (BRS/LVE, Inc. model SEC-002); internal measurements were 36.0 high × 30.5 wide × 35.0 cm deep. The intelligence panel of each chamber contained three 2.5-cm response keys, which were 8.5 cm apart (center to center) in a row, 26.0 cm above the chamber floor. Only the two side keys were used; each key could be transilluminated yellow, red or green. Key pecks of approximately 0.25 N of force were counted as responses. There were three houselights located 6.5 cm above the center key (red, white, and green); only the white houselight was used. Milo could be presented via a hopper through a 5.0 cm × 6.0 cm opening, which was located 11.0 cm directly below the center key. Each chamber was equipped with an exhaust fan for ventilation, and white noise was present in the room during sessions to mask extraneous sounds. Experimental events were programmed and data recorded by a Windows-based computer using Med Associates 4.0® (Georgia, VT) software and interface equipment located in an adjacent room; programming and recording occurred at a 0.01-s resolution.

2.3. Behavioral procedure

Because of the pigeons' prior experience, no training was required. Each session consisted of a seven-component mixed schedule; during components, the left and right-key lights were transilluminated yellow, and the white houselight was on. Each component consisted of a dependent VI 27-s concurrent schedule and arranged a different reinforcer ratio. The programmed reinforcer ratios were (left:right; 27:1, 9:1, 3:1, 1:1, 1:3, 1:9, 1:27). There were 10 interval values, determined using a Fleshler and Hoffman (1962) exponential progression; each interval was used once per component. At the beginning of a component and after each reinforcer, a key was selected with the probability determined by the programmed reinforcer ratio in effect for that component. The first peck to that key after the interval had timed out operated the hopper for 2.5 s. When the food hopper was raised, the opening was illuminated and all other lights in the chamber were extinguished. There was a 2-s change-over delay (COD) arranged such that a peck could not produce reinforcement until 2 s had elapsed since a change-over response. Components were randomly selected, occurred once per session and were separated by 10-s blackouts. Sessions were conducted 7 days a week and lasted until all 70 reinforcers had been delivered or until 75 min had elapsed, whichever occurred first.

2.4. Pharmacological procedure

Drug dosing began after approximately 200 sessions under the behavioral procedure (thus, when combined with their previous experience of 100 sessions, the pigeons had been exposed to over 300 sessions under this procedure prior to drug testing). *d*-Amphetamine sulfate (Sigma) was dissolved in saline. Injections (i.m.) occurred 15 min before selected sessions and were in a solution volume of 1.0 ml/kg. Injections occurred as long as data from the previous day were within control range; injections were separated by at least 3 days. The doses tested (expressed as total salt) were 0.3, 1.0, 1.8, 3.0, and 5.6 mg/kg; because of substantial effects on overall response rates at 3.0 mg/kg, Pigeon 49889 did not receive 5.6 mg/kg. Initial doses were administered in an ascending order for Pigeons 280 and 17560 and in a descending order for Pigeons 8418 and 49889. Upon completion of one determination of each dose, doses were administered again in an order opposite to the initial dose-effect curve for each pigeon. Subsequent dose administrations were given in a mixed order. Each dose was administered a minimum of 4 times (except 5.6 mg/kg, which completely eliminated