

A DETAILED ANALYSIS OF THE EFFECTS OF METHAMPHETAMINE ON
SCHEDULE-CONTROLLED RESPONDING IN PIGEONS

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ABSTRACT

In behavioral pharmacology, overall response rate is the measure most often used to study the effects of drugs on an animal's ongoing operant behavior. However, it has been argued that an overall measure of response rate may not provide the most valid description of behavior and, thus, a more detailed analysis might prove beneficial in classifying drug effects. The purpose of the present research was to (1) study effects of methamphetamine on schedule-controlled responding, (2) determine if a log-survivor analysis recently used to study nose-poke responding in rats could be extended for use with key-pecking in pigeons and (3) examine microproperties of pigeon responding using an IRT analysis. Pigeons were trained to peck a lighted key under a multiple random-interval (RI) 1-min, RI 4-min schedule. Interresponse times (IRTs) were collected and then analyzed via log-survivor plots and an analysis described by Blough (1963) and used in greater detail by Palya (1992). Log-survivor plots show the proportion of IRTs greater than some time as a function of time in the session. The IRT analysis involved graphing each individual IRT as a function of its temporal position within the interval. Several doses of methamphetamine were administered (0.3 – 5.6 mg/kg) and the effect on both summary measures (overall response rates) as well as the more detailed analyses was observed. Log-survivor analyses did not produce the “broken-stick” responding seen in previous studies with rats and quantitative measures of bout-initiations and within-bout responses could not be obtained. The IRT plots showed clear bands of responding at 350 ms and 700 ms and responding in the initial (350 ms) band was affected more than responding during other bands or at other IRTs. These results strengthen the argument that not all responding (various IRTs) is uniformly affected by methamphetamine administration and suggest that a detailed analysis of responding might prove more useful than summary measures in characterizing drug effects on behavior.

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DEDICATION

I would like to dedicate this thesis to my mother, grandmother and grandfather. Without their continued and unwavering support and guidance through the years, the completion of this project would not have been possible.

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INTRODUCTION

As a result of its close relationship with the experimental analysis of behavior, behavioral pharmacology's primary interests differ from those commonly associated with psychology (i.e. mental constructs). Within behavioral pharmacology, drug effects generally are not considered to be a result of underlying and unobserved processes (e.g., craving, motivation, and/or internal states); indeed, the use of hypothetical constructs to describe the effects of drugs (e.g. anxiety reduction and increases in motivation) generally is avoided. Also, in contrast with general pharmacology, physiological effects of drugs are not the primary focus of many behavioral pharmacologists (although such effects are not dismissed as unimportant). Rather, a goal of behavioral pharmacology is to characterize specifically, through the use of experimental procedures and rigorous experimental control, how drugs affect instances of overt behavior. Therefore, instead of speaking of a drug effect in terms of a reduction in "anxiety," a behavioral pharmacologist might speak of the drug effect in terms of its tendency to increase or decrease the responding under conditions typically described as anxiety-inducing (e.g., Branch, 1991; Thompson & Schuster, 1968).

Instead of invoking mental or physiological mechanisms, behavioral pharmacologists often concern themselves with the "behavioral mechanisms" by which drugs affect behavior that is observable, quantifiable, and can come under experimental control (Blackman & Sanger, 1978; Branch, 1984; 1991; Dews, 1958; Thompson & Schuster, 1968). Thompson (1981) noted that:

Specifying the behavioral mechanism(s) responsible for an observed effect involves (1) identifying the environmental variables which typically regulate the behavior in question, and (2) characterizing the manner in which the variables' influence is altered by the drug (p. 5).

Hence, according to this view, drugs are capable of producing observable effects on behavior not only by altering the behavior itself (e.g., altering the organism's ability to perform the required task), but also by altering the way in which the environment controls behavior.

Drug effects have been shown to be a function of a number of different environmental variables, such as: the schedule of reinforcement currently maintaining behavior, the type of reinforcer presented, past behavioral or pharmacological history, and environmental consequences occurring in temporally removed situations. Indeed, a single drug may have drastically different effects on responding depending on the context in which it is administered (e.g., Branch, 1984; 1991; Thompson & Schuster, 1968). This control can be manifested regardless of whether the conditions responsible for the effect (e.g., behavioral or drug histories) are present or removed from the immediate situation. As a result of these multiple influences on behavior, drugs can alter behavior in a number of different ways. For example, one drug may decrease (or increase) the organism's ability to emit a specific response by altering motor coordination. Another drug may alter sensory perception of stimuli by the organism, whereas another might alter the control of behavior by events that have been or currently are contingent on the organism's responding. Any of these variables might facilitate or hinder performance of the target response.

Behavioral pharmacologists often implement three-term operant contingencies (Malott & Trojan Suarez, 2004; Mazur, 2002; Skinner, 1969) in order to obtain behavioral baselines and

characterize the effects of environmental manipulations (generally drug administration) on operant behavior. The “three-term” contingency, fundamental to the study of operant conditioning, specifies:

- (1) the context in which a response can occur (antecedents: discriminative stimuli)
- (2) the operant (target) response
- (3) the stimuli following the response (consequence: reinforcer or punisher)

Therefore, behavior may come under control of the contingency in the following manner: in the presence of a certain antecedent stimulus (e.g., a green light), a certain consequence (e.g., food) is provided following a certain response (e.g., lever press). As a result of such a contingency, the target response is more likely to occur in the presence than in the absence of that stimulus and, thus, the behavior has come under control of the operant contingency.

The use of these contingencies under controlled experimental conditions provides behavioral pharmacologists with instances of reproducible behavior that are amenable to pharmacological manipulation. In a typical experimental arrangement, a food-deprived animal is placed into an experimental chamber and its responses (e.g., lever presses or key pecks) are reinforced on some schedule via the presentation of food. Once a consistent pattern of behavior has been established, a dose of drug is then administered. Because drug conditions are planned to differ from baseline conditions only in the presence of the independent variable (dose of drug), the observed changes in that behavior (often the rate of its occurrence) are said to be entirely a result of the introduction of the independent variable. Through the use of these precise and controlled methods, behavioral pharmacologists have made substantial progress in identifying the principles of drug action on behavior (e.g., Blackman & Sanger, 1968; Branch, 1984; Branch, 1991; Thompson & Schuster, 1968).

Behavioral Effects of Drugs

Many variables that determine drug effects are purely pharmacologic (e.g., dose, presence of other drugs, route of administration). Many, however, are behavioral. It is not uncommon to speak as if drugs have inherent effects on behavior. For example, one might often refer to a particular drug as being classified as either a “stimulant” or a “sedative” (see Maisto, Galizio & Connors, 1999). Classifying drugs in such a manner implies that a given drug will produce a consistent effect on a given behavioral measure, regardless of the conditions under which that behavior occurs. Nearly 50 years of research in behavioral pharmacology, however, has illustrated that drugs do not have inherent effects on behavior. Rather, as stated earlier, observed drug effects are a result of interactions among a number of different variables, including environment/behavior relations.

An important variable that affects how drugs alter behavior is the schedule of reinforcement. This type of effect was shown in a landmark study conducted by Dews (1955). Key pecking by two pigeons was maintained under a fixed-ratio (FR) 50 schedule, whereas key pecking by another two pigeons was maintained under a fixed-interval (FI) 15-min. These two schedules engender different rates and patterns of behavior – a higher rate during the FR 50 and a lower rate during the FI 15-min schedule. Several doses of pentobarbital sodium were administered after stable baselines were obtained in all birds. Interestingly, the effects of the drug on the rate of responding were highly dependent on the schedule of reinforcement controlling behavior. Pentobarbital was shown to act as either a “stimulant” or a “depressant,” depending on the schedule. Following administration of 1.0 and 2.0 mg/kg, response rates maintained by the FI 15-min were decreased, whereas response rates maintained by the FR 50 were increased. The

results of this study suggest that the schedule of reinforcement determines, at least to some extent, the effect of a given drug on operant behavior.

More evidence of schedule-dependent drug effects was found when McMillan (1968) studied the effects of several sympathomimetic amines (e.g., *d*-amphetamine and ephedrine) on responding under multiple FR FI schedules. The multiple schedule was comprised of FR 30, FI 5-min, and FI 15-min components, each in the presence of a distinct stimulus. During baseline, higher rates of responding were observed in the FR schedule when compared to the FI schedules. The effects of both *d*-amphetamine and ephedrine were shown to depend on administered dose, as well as the schedule of reinforcement in effect. Low doses of these drugs increased response rate in both interval schedules, whereas the same doses decreased response rate during the ratio schedule. Evidence of this control of drug effects by schedule of reinforcement has been observed in numerous other studies (e.g., Clark & Steele, 1966; Sanger & Blackman, 1975; Waller & Morse, 1963).

A great deal of attention has been devoted to understanding the basis of schedule-dependent drug effects. In a frequently cited study, Dews (1958) investigated the effects of methamphetamine under several different schedules with pigeons. Birds were trained either on a variable-interval (VI) 1-min, an FR 50, an FI 15-min, or an FR 900 schedule. During baseline, two of these schedules (VI 1-min and FR 50) produced high overall rates of responding, whereas the other two (FI 15-min and VR 900) produced lower overall response rates with periods of responding alternating with periods of non-responding. A series of methamphetamine doses was administered after stable baselines were observed in each schedule. Interresponse times (IRTs; the periods of time between responses) were recorded during control and drug sessions. Dews found that low doses of methamphetamine tended to decrease long (i.e., > 5 s) IRTs in number

and length, while larger doses tended to increase the length of short (i.e., < 1 s) IRTs. Because FR 50 and FR 900 are the same type of schedule, differing only in the control rates of behavior that they engender, the fact that they yielded very different drug effects led Dews to suggest that control rate of responding, rather than schedule of reinforcement, was a better predictor of drug effects. The ability to predict drug effects based upon control rate of responding has considerable generality and, thus, has come to be known as the “rate-dependency” principle (e.g., Dews & Wenger, 1977; Sanger & Blackman, 1975).

Given that different control response rates typically result from different rates of reinforcement, it is possible that the basis of schedule-dependent drug effects relates to the control rate of reinforcement, rather than the control rate of responding. Lucki and DeLong (1983) isolated control rate of responding from control rate of reinforcement in order to determine which of these variables was responsible for the effects seen when *d*-amphetamine was administered to rats. At any time during the experiment, either the control rate of responding or the control rate of reinforcement was held constant while the other was varied, or allowed to vary. To equate reinforcement frequency, a standard VI schedule was yoked to reinforcement rates generated under a differential-reinforcement-of-low-rate (DRL) 7-s schedule. This manipulation yielded different control rates of responding in each schedule (rates under the VI schedule were much greater than those under the DRL schedule). Results showed *d*-amphetamine to have differential effects depending upon this difference in control rate of responding; increases in response rate were seen under the DRL schedule, whereas decreases in response rate were observed under the VI schedule when drug was administered. In order to equate control rates of responding, random-ratio (RR) schedules were implemented, each with their own probability of reinforcement. A multiple RR 20 RR 50 schedule was in effect in which

the probability of reinforcement for each response was 0.5 and 0.2, respectively. This manipulation ensured that control rates of responding were kept approximately equivalent, while allowing rate of reinforcement to vary. Results showed that effects of *d*-amphetamine were equivalent (dose-dependent decreases in response rate) between the two schedules when only rates of reinforcement were varied and control response rates were held constant. These results suggest that control rate of responding, rather than control rate of reinforcement, was the primary determinant of the effects of *d*-amphetamine.

Because of effects such as those reported by Dews (1958), McMillan (1968), and Lucki and DeLong (1983), much of behavioral pharmacology has focused on investigating the nuances of the rate-dependency principle. According to the rate dependency principle, it is not the schedule of reinforcement per se but the rate of responding engendered by the schedule that is the important determinant of drug effects on schedule-controlled operant behavior. One common way of investigating this effect utilizes FI schedules. With this method, response rates at different points within the interreinforcement interval (IRI) are obtained. It has been found that different rates occur during different points of an FI schedule (prior to drug administration): (1) low rates tend to occur early in the interval, (2) moderate rates tend to occur in the middle of the interval, and (3) higher rates tend to occur toward the end of an interval (see Branch, 1991). Dividing the FI schedule into 10ths, for example, allows the experimenter to analyze drug effects on several different control rates. Of interest, then, is the change in average rates during these segments of the interval when drug is administered. When the percentage of control response rate is plotted as a function of the average rate of reinforcement on log-log coordinates, the resulting plot reveals the general idea of rate-dependency (Figure 1). A horizontal line at 100% on this graph indicates no change from control to drug conditions as a function of rate of

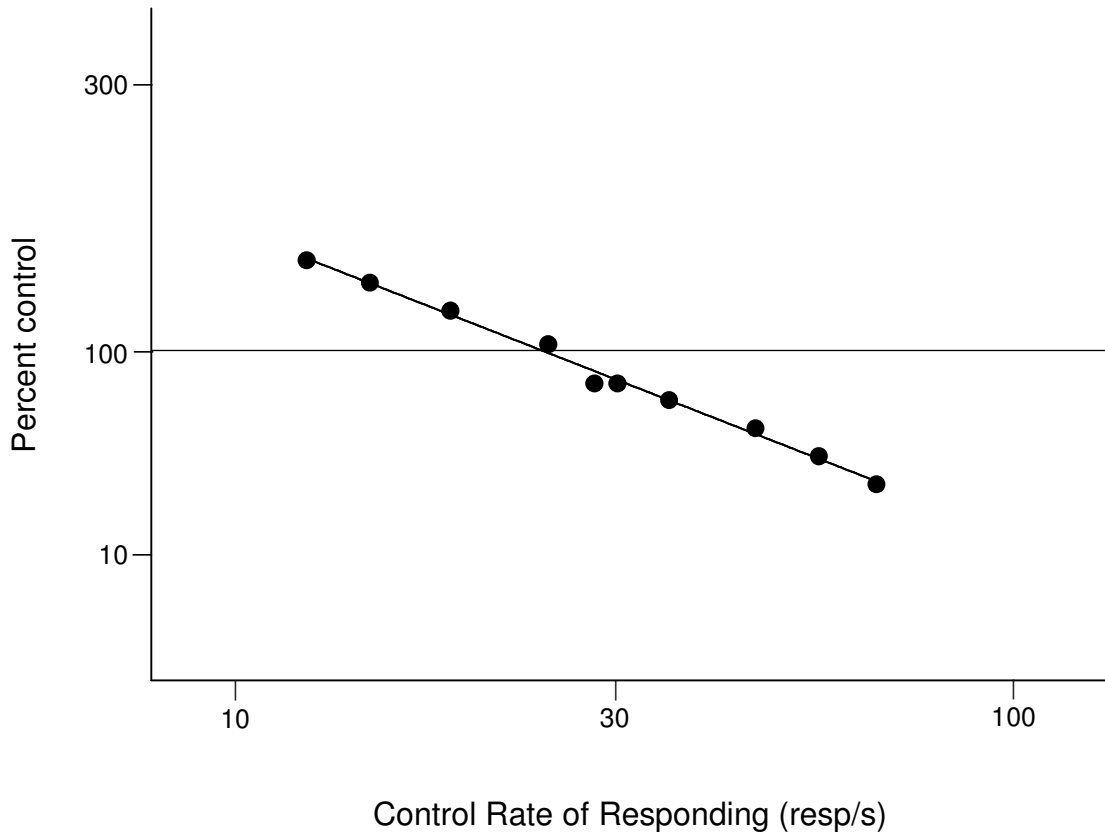


Fig. 1. Sample rate-dependency plot. Percent control is presented as a function of control rate of responding in responses per second on a log-log scale. In this example, lower control rates of responding are increased and higher control rates of responding are decreased by drug administration.

responding. However, the pattern typically produced when fitting a regression line to data produced by this procedure, is that of a straight line with a negative slope. The negative slope in Figure 1 indicates that lower response rates (e.g., rates early in an FI) are increased, whereas higher response rates (e.g., rates later in an FI) are decreased when drugs are administered. Intermediate doses of a number of drugs, particularly the so-called stimulants (e.g., *d*-amphetamine, methamphetamine, and cocaine), have been shown to increase the lower rates early in the interval, while causing no change or a decrease in the high rates that occur later in the interval, an effect consistent with rate-dependency.

Although rate-dependency may be regarded as an important empirical principle that has allowed behavioral pharmacologists to predict drug effects on operant behavior under certain conditions, like most analyses of drug effects on operant behavior, it relies on overall response rates to make its predictions. There have been some suggestions that overall response rate might not always provide the most effective characterization of drug effects on behavior (e.g., Branch and Gollub, 1974; Weiss and Gott, 1972; Ziriax, Snyder, Newland and Weiss, 1993). In making this point, researchers have shown that the classification (and interpretation) of drug effects and their determinants vary drastically, dependent on the type and level of the analysis implemented. As a result, these researchers have advocated the use of detailed analyses in order to reveal order at a more microscopic level than that provided by aggregated response rates.

In an important study, Branch and Gollub (1974) conducted a detailed analysis of *d*-amphetamine's effects under FI schedules. Groups of three pigeons had been trained to peck lighted keys and each group was exposed to one of three FI schedules of food presentation (FI 40 s, FI 100 s or FI 300 s). Doses of *d*-amphetamine were administered once stable key-pecking was observed and analyses were conducted at a number of levels in order to determine how to best

characterize behavior during a session of responding. Analyses of *d*-amphetamine's effects on overall rate, on rates at different moments in the schedule, and on acceleration during the FI were performed. Consistent with the predictions of rate-dependency, control rates were good predictors of the effects of *d*-amphetamine in corresponding parts of the FI. However, this was limited to the beginning and end of the intervals, as well as instances in which averages were taken over a number of intervals. Branch and Gollub suggested that responding, especially in the middle periods of the FI schedule, was bimodal in nature and contained either high or low rates of responding, which were masked by averaging rates during these portions of the interval. The implication was that "rate-dependency" under FI schedules was an artifact of averaging. Therefore, at least on FI schedules of reinforcement, overall rate did not provide the most accurate characterization of responding. These findings suggest that microscopic analyses might prove useful in characterizing schedule-controlled responding and in classifying effects of drugs on behavior.

Gentry, Weiss and Laties (1983) conducted a molecular analysis of responding in pigeons during two FI schedules (FI 5- and FI 15-min) of reinforcement. Fixed-interval schedules were chosen because of the "scallop" patterning that is observed when response rates are reproduced graphically. This scalloped responding has commonly been described as an acceleration of response rates throughout the interval (i.e., the organism is responding faster as time passes in the interval). Analyses of individual IRTs obtained on FI schedules showed no clear evidence of the accelerated responding often associated with FI schedules. Rather, exclusion of the longest IRTs (IRTs > 20 s) during the interval reduced the index of curvature associated with average FI responding, suggesting that these long IRTs (alternating early in the interval with bursts of responding) were responsible for the "scalloped" responding often observed during these

schedules. There was no evidence of the pattern one would normally see if acceleration (longer IRTs shifting towards shorter IRTs) were occurring within individual intervals. The analyses performed by Gentry et al. lead to the suggestion that behavior on interval schedules can be classified in three states: pausing following reinforcement, interim behavior (relatively short IRTs occurring with the same frequency throughout the interval) and terminal behavior (a rise in moderate length IRTs as time in the schedule elapses). Thus, as with Branch and Gollub's (1974) findings, these data suggest that averaging to obtain overall rates can mask important characteristics of behavior occurring within an interval.

Other studies have investigated the importance of a microscopic analysis in the description of drug effects. For example, Weiss and Gott (1972) examined effects of *d*-amphetamine, pentobarbital, and imipramine on responding in pigeons maintained by an FR 30 schedule of food presentation. Individual IRTs within each IRI were collected and analyzed as a function of ordinal position in order to characterize the effects of these drugs throughout the ratio. Amphetamine and imipramine both acted to increase the length of first IRT of each ratio, while pentobarbital decreased this IRT. The remaining IRTs of the ratio schedule were differentially affected according to their position in time and it was clear that three groupings of IRTs occurred within the ratio. Weiss and Gott suggested that this may be a result of three different types of responses occurring within the ratio: (1) "nibbles" – closing and opening the beak rapidly; (2) "clean" pecks of the key; (3) "harmonics" – which result from IRTs that contain clean pecks that miss the key. Amphetamine and imipramine both eliminated the first cluster of IRTs (nibbles), decreased and shifted to the right the distribution of clean pecks, and shifted the harmonic cluster to the right. These data again argue for a more detailed analysis in the study of drug effects.

In another study highlighting the importance of detailed analyses of the behavioral effects of drugs, Ziriak et al. (1993) examined the effects of amphetamine on concurrent stochastic reinforcement of waiting (SRW) schedules in two adult female monkeys. In SRW schedules, which are quite similar to VI schedules, reinforcement rate is held constant as long as the IRTs emitted are less than the value selected for the schedule. The probability of reinforcement increases at the same rate for all IRTs less than the value selected for the schedule (reinforcement is provided at a rate of 1 per 'x' seconds – 'x' being the value of the SRW schedule). Each subject was exposed to a concurrent SRW 20 s SRW 80 s schedule and, once stable baselines were obtained, several doses of *d*-amphetamine were administered. Analysis of response rates showed that amphetamine produced dose-related decreases in overall response rate as well as rates of switching between schedules. However, a more detailed analysis of IRTs revealed that these changes in both components of the concurrent schedule were a function of a drug-induced lengthening of relatively short IRTs, rather than a uniform effect on all IRT durations. Therefore, though analysis of overall rates seemingly showed orderly results, this was a result of order at a more molecular level in the session.

The data reported by Weiss and Gott (1972), Branch and Gollub (1974), Gentry et al., (1983) and Ziriak et al. (1993) illustrate the importance of level of analysis in characterizing drug effects and in determining the theoretical interpretations of them. That is, the level of analysis can determine the specific interpretations made. The results of these studies suggest that drug effects on schedule-controlled operant behavior should be analyzed in a variety of ways, over and above that provided by overall response rates.

Response Rate as a Component Measure

Other researchers also have suggested that overall response rate may not always be the most appropriate level of analysis (e.g., Gilbert, 1958; Mechner, 1992; Mechner & Hyten, 1997; Shull, 1991). For example, Gilbert (1958) conceptualized operants as being divided along several different dimensions. One of the dimensions that Gilbert identified was *perseveration*, or the period of time one spends engaged in some reinforced task. This perseveration is said to vary throughout the time in which an organism is responding. According to this view, individual responses differ on at least two dimensions and may be classified as to whether they: (1) *initiate* a period of perseveration or (2) occur *within* a period of perseveration. If this is true, then it is quite possible that each of these dimensions could be differentially affected by some single manipulation, even though changes in overall response rate may appear similar. For example, a given drug could affect either of Gilbert's dimensions in a number of different ways. If this is indeed possible, then one might argue that treating response rate as a single unit of behavior could result in a clouded view of what is actually occurring within an experimental session.

Recently, Shull and his colleagues have expounded on the idea proposed by Gilbert (1958) (Shull, Gaynor & Grimes, 2001; Shull, Gaynor & Grimes, 2002; Shull, Grimes & Bennett, 2004). In this two-mode conception of operant response rate, overall response rate is comprised of two distinct response types: periods of engagement which alternate with periods of disengagement. For example, a rat may begin to press a lever (an engagement or bout initiation), press for approximately 20 s at a fast rate (responses within the bout), and then may engage in some other activity, such as grooming (a period of disengagement). This idea can be characterized with a simple event record of responding (Figure 2). Responding in this event record can feasibly be divided into periods of engagements and disengagements. In examining

Event record of rat nose-poke behavior

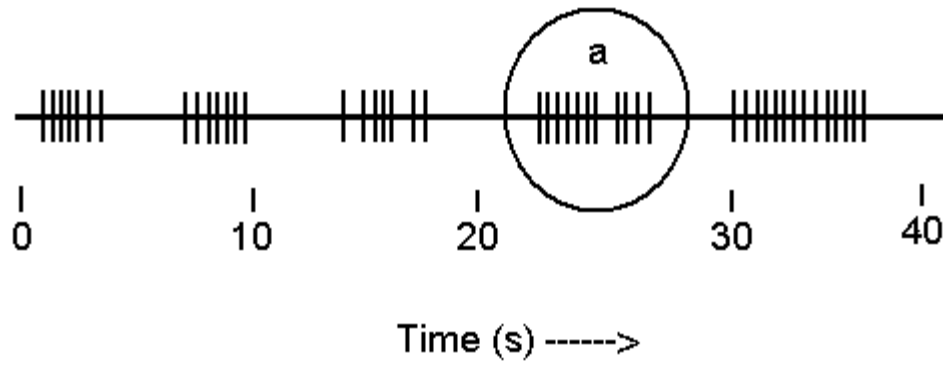


Fig. 2. Sample event record of rat nose-poke responding; Included to illustrate the arbitrary nature of visually selecting where a bout may begin and end. Adapted from Shull et al. (2001).

the cluster of responses at point “a,” one could conceivably name this entire cluster a period of engagement separated from other responding by the breaks at the beginning and end of “a.” However, without a quantitative method to define these periods of engagements and disengagements, one could also make the argument that there are two separate periods of engagement during “a.” Regardless of the method used to dissect response rate into these clusters, these separate components are said to combine to yield an overall measure of behavior (response rate). Because response rate may be a composite measure and not a unitary one, as we often consider it to be, using a single overall measure may not give an accurate depiction of the structure of behavior occurring within a session. The variations that we observe in response rate may be a function of our manipulations having differential effects on these components of responding. Some variables may affect the tendency to initiate a bout, while others may affect the number of responses occurring within a single bout. However, both types of variables may serve either to increase or decrease overall response rate. This framework implies a need to break down response rate into its individual components and measure the bout initiation rate as well as the number of responses per bout.

Dissection of Response Rate into its Component Parts

Log-survivor plots appear to be a useful method with which to analyze behavior into its component parts. It has been shown through these plots that behavior, specifically response rate, can be divided into its component parts via the analysis of IRTs (Berdy, 1993; Tolcamp & Kyriazakis, 1999). In log-survivor plots, the proportion of IRTs longer than some time (t) is plotted on a logarithmic scale as a function of time (t) on a logarithmic scale. These plots provide a method for determining if operant responding reveals the two-mode conception of response rate described above. Log-survivor plots have recently been used to separate overall response

rate into: (1) rate of bout initiations and (2) number of within-bout responses (Shull et al., 2001; 2002; 2004).

Shull et al. (2001) trained rats to emit nose-poke responses under various interval schedules of food presentation. Interresponse times were then analyzed and log-survivor plots were constructed from the data. These plots from rat data were strikingly similar to log-survivor plots obtained in previous computer simulations. During these simulations, both the rate of initiations and the number of within-bout responses were manipulated individually via probability generators in order to observe the resulting log-survivor plots. This suggests that the animals in this experiment respond in a manner similar to this two-state model of responding. These simulations suggested that the log-survivor analysis may be an appropriate method for splitting response rate into these two component parts.

Rats' nose-poking in the Shull et al. (2001) study resulted in two distinct distributions of IRTs which were revealed nicely using log-survivor plots. In graphing these distributions, a "broken-stick" appeared (Figure 3). That is, there is (a) a steep drop resembling the "blade" prior to about 1 s, followed by (b) a break and a more gradual decline (the "shaft" of the stick). The steep drop shown here represents a distribution of short IRTs, characteristic of rapid responding within a bout. The second, more gradual, portion of the function shows a distribution of longer IRTs, characteristic of responses that end periods of disengagement (e.g., bout initiations).

Fitting a line to a stable portion of the right hand limb provides measures of both bout initiations as well as the number of responses occurring per bout. The slope of the fitted line can be interpreted as the rate of initiations. When this line is extracted back to its intercept on the y-axis, the value of this intercept represents the proportion of all responses that are bout initiations. Therefore, the inverse of this value can be interpreted as the number of responses occurring per

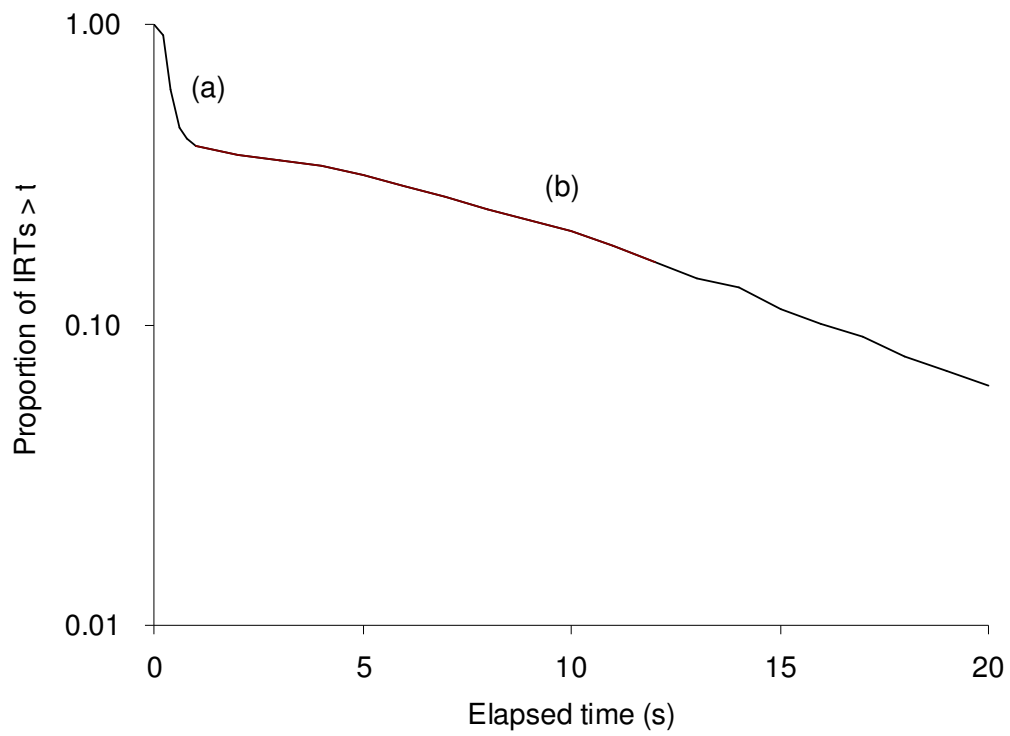


Fig. 3. Example of a log-survivor plot. Log proportion of IRTs longer than some time are plotted as a function of elapsed time - 'a' and 'b' represent the within-bout and bout-initiation limbs, respectively.

bout. In Figure 3, the first leg of the graph (a) represents rapid responding or responses occurring within a bout, whereas the more gradual decline (b) represents a slower rate of responses or the bout initiation rate.

Graphically, a change in the rate of bout initiations is indicated in the log-survivor plot by a change in the slope of the right hand limb; a steeper slope represents a higher initiation rate (triangles versus circles in Figure 4). On the other hand, a change in the number of responses within a bout results in a change in the y-intercept (Figure 5). An increase in the number of responses during a bout would be represented graphically by a steeper drop in the initial limb of the log-survivor plot (triangles versus circles in Figure 5). In each of these figures, it is important to note that overall rate may be changed by the same amount (from low to high initiation rates and from short to long visits) by each manipulation. However, a difference in rates in Figure 4 could be created entirely by an increase in initiation rates, whereas a difference in rates in Figure 5 could be created by an increase in within-bout responding.

Shull et al. (2001) used a log-survivor analysis to characterize nose-poking in rats under various VI schedules of reinforcement and examined effects of: (a) rate of reinforcement (VI 1 min vs. VI 4 min), (b) magnitude of reinforcement (1 vs. 4 pellets), (c) percentage of obtained reinforcers that were contingent on responding (25% vs. 100%), and (d) addition of a tandem FR requirement to the end of the VI schedule in effect. The manipulations applied by Shull et al. revealed that different types of variables affected within-bout responding and bout initiation rate differentially, even though, as stated earlier, they tended to affect an overall measure of response rate in much the same way. Of the manipulations above, three (i.e., altering the rate of reinforcement, the amount of the reinforcer, and the percentage of contingent reinforcers) were shown to affect the tendency to initiate bouts, leaving number of responses within bouts

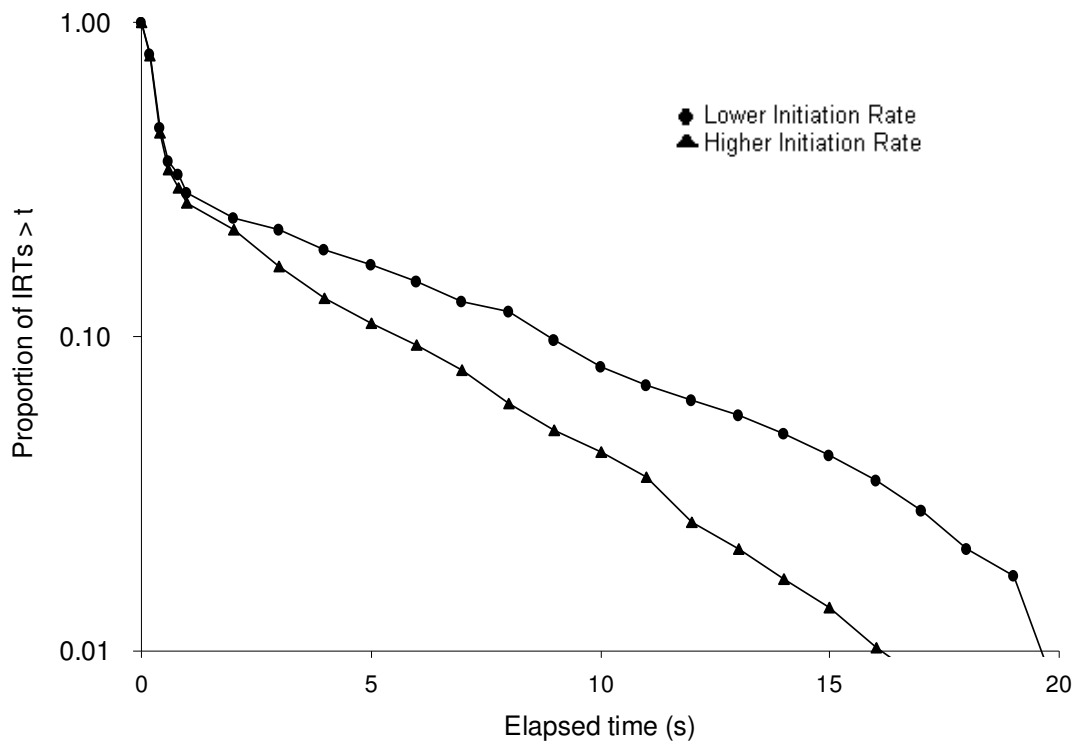


Fig. 4. Hypothetical log-survivor plot from a session in which bout-initiation rate was varied. Log proportion of IRTs longer than some time are plotted as a function of elapsed time. Triangles represent a greater rate of bout initiations and circles represent a smaller rate of bout initiation responses.

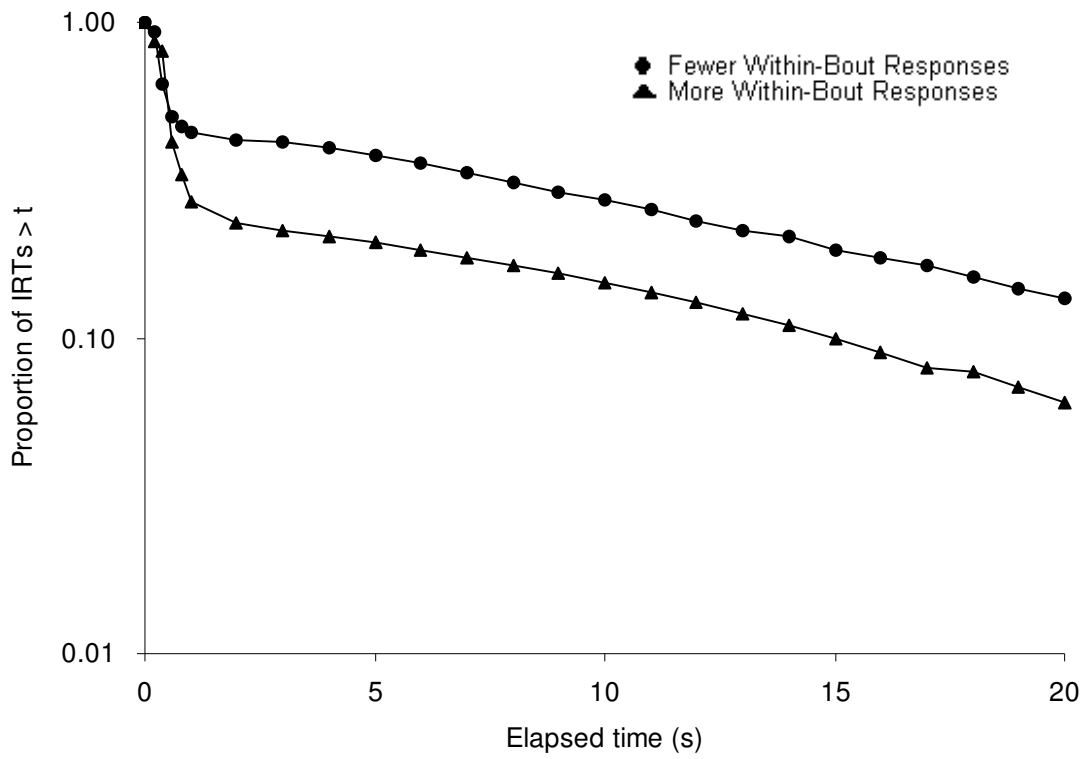


Fig. 5. Hypothetical log-survivor plot from a session in which the number of responses per bout was varied. Log proportion of IRTs are plotted as a function of elapsed time. Triangles represent a greater number of responses per bout and circles represent fewer responses per bout.

relatively unchanged. Changes in the behavior required by the schedule (e.g., adding a tandem FR requirement to a VI schedule) affected the number of responses per bout, but left initiation rates relatively unchanged.

In another recent study utilizing log-survivor plots, Shull et al. (2004) reinforced rat nose-poke responding on either a standard VI schedule of reinforcement or a tandem VI variable-ratio (VR) 4 schedule. Variable interval schedule values ranged from 15 s to 16 min. Analysis of the log-survivor plots indicated that responding, as in the study earlier, occurred in bouts and bout initiation rate was a function of programmed reinforcer rate. It should be noted, however, that in contrast with the previous study (Shull et al., 2001), within-bout responses were not systematically affected by the addition of tandem ratio requirements. Thus, the effects of this variable clearly require additional study. Nevertheless, the research by Shull and colleagues suggest that the two-state model can be useful for determining the effects of different variables on components of response rate.

IRT Analysis

Palya (1992) presented another type of analysis that had been previously used by Blough (1963) to analyze fine structures of responding. Pigeons were exposed to a variety of schedules (VI, VR, FI, FR, DRH and DRL) and the resulting performances were analyzed in several ways. One of these analyses included the graphing of each individual IRT as a function of time in the IRI (see Figure 6). Each individual point of these graphs indicates an IRT; its position on the *y*-axis indicates the value of the IRT and its position on the *x*-axis indicates the temporal position within the IRI (these plots will be referred to henceforth as simply 'IRT plots'). These plots showed clear order at a more detailed level than that provided by overall rate of responding. Palya noted that a band (recurrent responding at a specific IRT) of responding in each of the

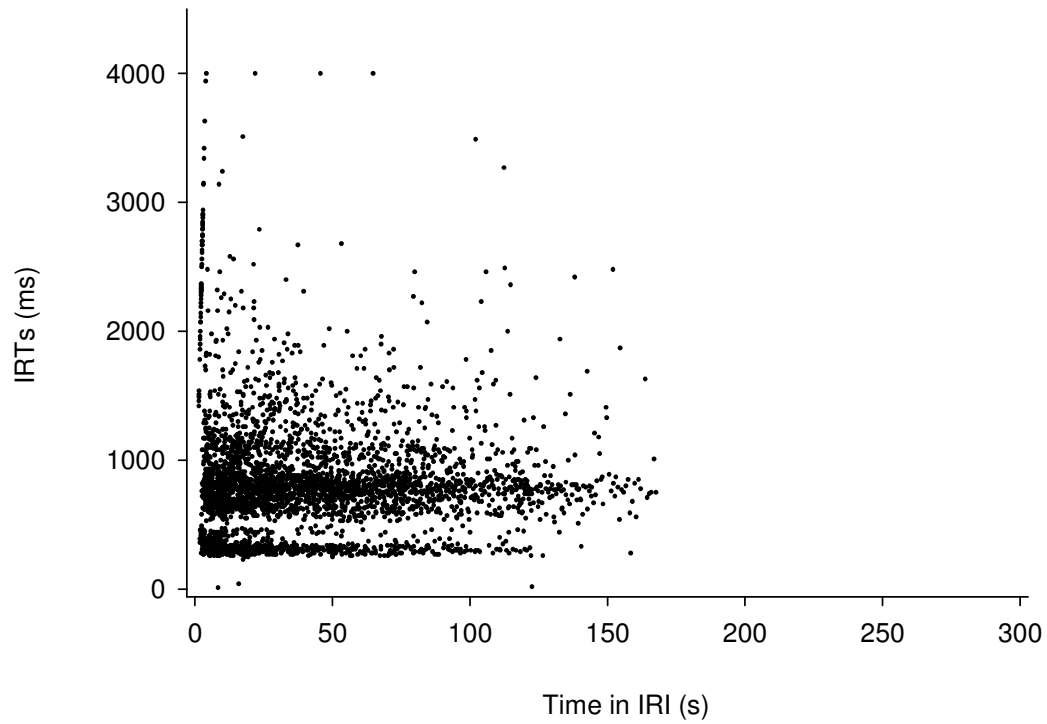


Fig. 6. Sample IRT plot: graph of each individual IRT as a function of time in the IRI. All IRTs greater than 4000 ms are represented as 4000 ms. These graphs reveal the tendency of subjects to emit recurrent responding at specific IRT values.

schedules occurred around 350 ms for each bird in all schedules. With the exception of the DRL schedule, “bands” of responding also occurred at multiples of 350 ms (i.e., 700 ms and 1050 ms) for several of the subjects. Overall rate of responding was largely determined by the responding occurring within these first few bands of IRTs. Palya also noted that several of the subjects produced a band of responding at shorter IRTs (< 350 ms) than those in the main band of IRTs. In order to analyze these bands of responding and determine if they were an artifact of the properties of the key (e.g., key-bounce), Palya conducted analyses with several types of switches. None of these manipulations served to eliminate this band of extremely short IRTs. Computer simulations were run in order to better understand the recurrent patterns of responding seen in these plots. Through observation, Palya concluded that many of the birds were pecking at the key with IRTs that would have fallen into the main bands (350 ms) of responding but did not contact the key for one reason or another; either they were head movements in the direction of the key were not drastic enough to contact the key, pecks that were directed away from the key, beak openings, and/or body movements that did not resemble pecking motions. A simple recurrent pulser was used and produced responding at 350 ms and 35% of pulses were randomly deleted in an attempt to recreate the bands of responding lying above the main band. Responding produced by this computer simulation was similar to that of the actual subjects with the exception of the IRTs falling below the main band of responding, which were present in the actual subject output but not in the simulation. These bands of responding that Palya observed might be considered the equivalents of the three types of responding discussed by Weiss and Gott (1972): nibbles (IRTs falling below the main band of responding), clear pecks (IRTs of 350 ms) and misses (resulting in the harmonic values of the main band). These plots, though they do not provide a quantitative

measure of these different types of responding, could possibly reveal important information about microstructures of behavior and the effects of drugs on these microstructures.

Rationale

The purpose of the present study was three-fold: 1) to see if a log-survivor analysis generalizes from rats' nose-poking to pigeons' key-pecking (i.e., whether a "broken-stick" characterization appears for pigeons), 2) to compare that analysis to the analysis described by Payla (1992), and 3) to determine if drug effects on schedule-controlled operant responding may be more precisely analyzed via the use of these more detailed analyses. As mentioned earlier, a majority of studies in behavioral pharmacology have relied on overall response rate to characterize drug effects on operant behavior. The studies providing more detailed analyses of drug effects reviewed above indicate that this sort of approach is useful and worth continued pursuit. Compared with analyses of overall rate of responding, analysis such as those offered by Shull and colleagues and by Palya may give us a more accurate idea of what is occurring once drugs have been administered to animal subjects. The effects of drugs on these two aspects of response rate (bout initiations and within-bout responses) have yet to be studied. It has been suggested that different variables affect different aspects of responding when using this analysis – variables affecting what the organism must do to obtain the reinforcer are expressed as changes in the number of within-bout responses, whereas changes in reinforcer properties (rate, magnitude, etc.) are expressed as changes in the rate of bout initiations. Thus, these sorts of data may shed light on whether a drug affects, for example, the organism's ability to respond (which might be evidenced by a change in within bout responding) or alters the effectiveness of the reinforcer (which might be evidenced by a change in initiation rate).

In line with data from rate-dependency analyses, one might assume that lower response rates (i.e., responses with longer IRTs) will increase via a shortening of the IRT. This would be revealed graphically by a steeper “shaft” on the log-survivor plot. Also, higher rates (i.e., responses with shorter IRTs) might be decreased via these short IRTs being lengthened after drug administration. Graphically, this would be revealed as a less steep initial drop in the “blade” of the log-survivor plot. These plots certainly seem to reveal a finer structure of operant responding and therefore remind us that more microscopic analyses might allow us to identify some of the behavioral mechanisms involved in rate-dependency.

Although the analyses used by Palya (1992) do not provide quantitative measures of responding, they can provide a picture of what may be occurring throughout the interval and how pigeon key-peck behavior is organized. If pigeon key-peck behavior is organized in a similar way to that found by Palya, methamphetamine might produce orderly effects on these bands of responding. If methamphetamine were to differentially affect these bands of responding (i.e., only affecting a certain band or increasing the frequency of IRTs in one band while decreasing the frequency of IRTs in another) this would serve to strengthen the argument that detailed analyses are important to accurately classify the effects of drugs on behavior.

Pigeons were trained on a multiple (random-interval) RI 1-min RI 4-min schedule of reinforcement and individual IRTs were analyzed via these two methods in order to determine if detailed analyses are important in the accurate classification of drug effects. The argument for the use of detailed analyses is strengthened if order is revealed at a more molecular level (than overall response rate) and if the administration of drug reveals effects that are dependent on the organization of responding at these levels.

METHOD

Subjects

The subjects were four male White Carneau pigeons (*Columba livia*), each identified by a number (2778, 541, 438 and 1944). Two of the pigeons (2778 and 541) were experimentally naïve and two (438 and 1944) had prior experimental and pharmacological experience. The pigeons were housed individually in a colony room. Lights operated on a 12:12 hour light/dark cycle (lights on at 7:00 a.m.) and experimental sessions were conducted during the light cycle and at the same time of day. Water and health grit were freely available in each of the home cages and pigeons were maintained at 80% of their free-feeding weights via supplemental feeding in the home cage.

Apparatus

Two identical experimental pigeon chambers were used. Each of these chambers measured 35.0 cm deep, 30.5 cm wide and 36.0 cm high and contained one response key, which could be trans-illuminated red, green or yellow. The response key was centered on the front wall, 26.0 cm from the floor of the chamber. A hopper, which provided controlled access to mixed grain (Purina[®]), was located 11.0 cm below the response key and a house light (1.2-W) was located 6.5 cm above the center response key. During presentation of grain, the hopper light was illuminated and all other lights were switched off. Each chamber contained a fan for ventilation and white noise was broadcast throughout the room in order to mask extraneous sounds. Experimental events were controlled and data were recorded via a Med Associates[®] interface and a Microsoft Windows[®] computer running Med Associates[®] software.

Behavioral Procedure

Random-interval schedules were selected because of their similarity to variable-interval schedules, which have previously been successfully used with the log-survivor analysis (Shull et al., 2001; 2002; 2004). A multiple RI 1-min RI 4-min schedule of reinforcement was implemented. These schedules were programmed by sampling a probability generator each second ($p = 0.01667$ for RI 1-min and $p = 0.00417$ for RI 4-min). When the probability criterion for the schedule in effect was satisfied, the next response produced reinforcement.

A unique key color was present during each component of the multiple schedule (P-438: red and green, P-541: green and red, P-1944: yellow and red, P-2778: red and green for RI 1-min and RI 4-min respectively). P-2778 and P-541 were magazine trained and key-pecking a single green center key was shaped. Because of their previous experience, P-438 and P-1944 were excluded from this portion of the procedure and began the next part of the procedure. After a single session under FR 1, pigeons were placed on a multiple RI 2 s RI 2 s schedule. These values were raised gradually across sessions until final schedule values were reached. The first component (RI 1-min or RI 4-min) of each session was determined randomly and components alternated thereafter. With the exception of P-1944, components for all birds were in effect for 300 s and were separated by 30 s blackouts during which responding had no programmed consequences and were not recorded. P-1944 emitted more IRTs than could be collected for the program and, thus, the components for this bird were shortened to 180 s. Sessions ended after each component had been in effect five times.

Sessions usually were conducted 5 days per week. Once rates of behavior were determined to be stable in each component, as determined by visually inspecting the overall response rates across experimental sessions, the pharmacological procedure began. Data were

considered to be stable when response rates under each component showed minimal variability and no obvious trend across five consecutive sessions (P-2778, P-541 and P-438) or by the 50th session (P-1944). It is important to note that P-1944 responded at a higher rate during the RI 4-min schedule and, in an attempt to alter response rates such that P-1944 was responding more frequently during the RI 1-min schedule, several manipulations were made. These manipulations included altering the stimulus associated with the RI 1-min schedules (changing it from red to yellow) and changing the RI 4-min schedule to an RI 8-min schedule. Neither of these manipulations had any effect on overall response rate and the lean schedule was returned to its previous value: RI 4-min.

Pharmacological Procedure

After stable rates in both components were established, a range of doses of methamphetamine hydrochloride (Sigma[®]) and saline were administered in an irregular order. Saline always was administered first, followed by the range of doses. Injections (*i.m.*) were administered using a solution volume of 1.0 ml/kg. The administered doses of methamphetamine were as follows: 0.3, 1.0, 1.7, 3.0, and 5.6 mg/kg. This range is typically used when methamphetamine is administered in behavioral pharmacology studies (e.g., Pitts & Febbo, 2004). Doses of 3.0 and 5.6 mg/kg were only administered if rates of responding were not reduced to near-zero levels by other doses. On test days, pigeons were injected 15-min prior to the beginning of their sessions. Injections were always separated by at least two days and data from the session immediately preceding those with injections served as no-injection control. Each dose and saline was tested at least twice and no dose was tested a second time before all doses had been administered once. If the effects of a given dose were disparate (as determined via visual inspection) additional determinations of the effects of that dose were conducted.

Data Analysis

Several measures of responding were obtained, including overall rates of responding and individual IRTs. Overall rates of responding are commonly used when describing the effects of a drug on operant behavior and these rates were plotted in a dose-effect curve. Individual IRTs occurring during the session were collected and entered into a spreadsheet in Microsoft Excel. These data were then organized into 0.01s bins, converted into proportion of IRTs greater than each bin size and log-survivor plots were then constructed using the obtained data. This was accomplished by plotting the proportion of IRTs (on a log scale) greater than a given duration as a function of duration (on an arithmetic scale). From these plots, if functions showed the broken-stick type responding seen in earlier studies, rate of bout initiations and number of within-bout responses could be extracted according to the method mentioned earlier. The IRT plots described by Palya (1992) were constructed by plotting each individual IRT in a session as a function of its time in the IRI. These plots reveal bands of recurrent responding at certain IRTs throughout the interval and the effects of methamphetamine on these recurrent IRTs can be observed.

RESULTS

Control Performance

For three of the four subjects (P-438, P-541 and P-2778) responding came under control of the component stimuli; response rates were higher during the RI 1-min component than during the RI 4-min component (hereafter also referred to as the rich and lean components, respectively). P-1944 responded at a higher rate than other birds and his rates of behavior during the rich and lean components were very similar, with a slight tendency to respond at a higher rate during the RI 4-min component. Average control rates for each subject are presented in Table 1.

Table 1

Control rates of responding for each bird during RI 1-min and RI 4-min components.

Overall Response Rate (resp/min)		
Pigeon	RI 1min	RI 4min
P-438	63.00	29.61
P-541	45.96	36.73
P-1944	125.06	141.28
P-2778	41.66	29.21

Individual IRTs from 2 sessions were analyzed in order to determine if the log-survivor analysis (Shull et al., 2001) or the IRT plots described by Palya (1992) revealed order at a level more detailed than that of overall rates of responding. The two sessions with overall rates of behavior that minimized the total deviation from the mean overall response rate (averaged over all control sessions) were selected for analysis. Each individual IRT from these sessions was included in all analyses. Log-survivor functions for these control conditions are presented for each pigeon in Figure 7. Responding during the rich component is represented by larger dots and responding during the lean component is represented by smaller dots. For the most part, these log-survivor plots do not show clear evidence of a “broken-stick” pattern reported by Shull et al. (2001). Thus, it was not possible to fit regression lines to these data in order to obtain reasonable estimates of bout initiation rates and number of within-bout responses. This broken-stick pattern should be seen when these data are plotted on a logarithmic y-axis if responding during these schedules can be easily divided into these two distinct response distributions. Several of these survivor functions (e.g., P-438 and P-541 during both the rich and lean components) showed slight evidence of multiple-breaks occurring within the first 1-2 s on the *x*-axis. The similarities between the rich and lean components are also quite apparent in these graphs. Responses that follow short IRTs tended to occur with approximately the same relative frequency during the RI 1-min and RI 4-min components, as evidenced by the similarities in the first section (> 1 s) of the survivor functions. After this initial segment of the figure, the log-survivor functions for the rich and lean components begin to separate and show differing slopes. Once these functions separate, it is apparent in each subject’s data that the schedule providing the higher rate of reinforcement (RI 1-min) was accompanied by a steeper slope. With the exception of P-1944, a small

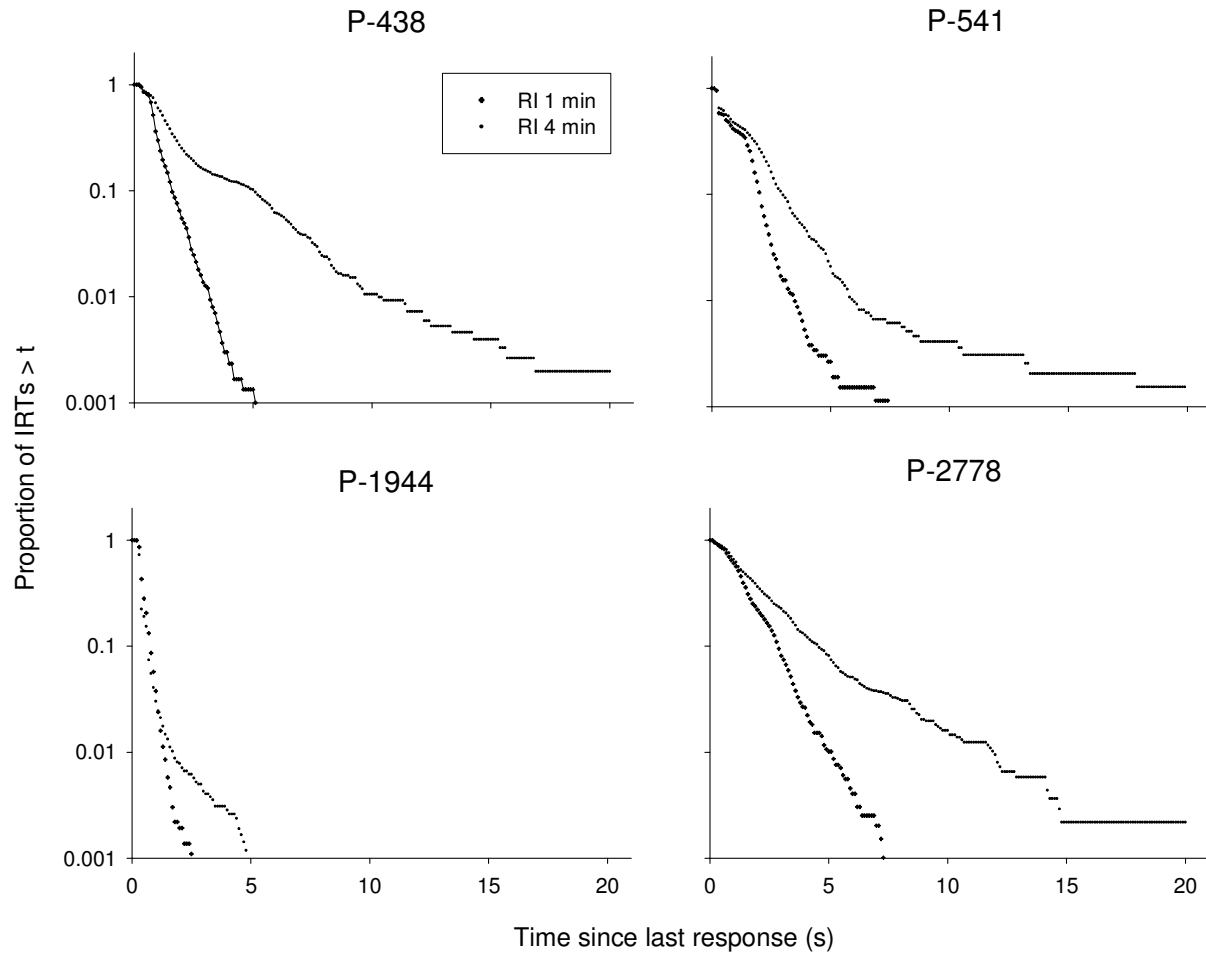


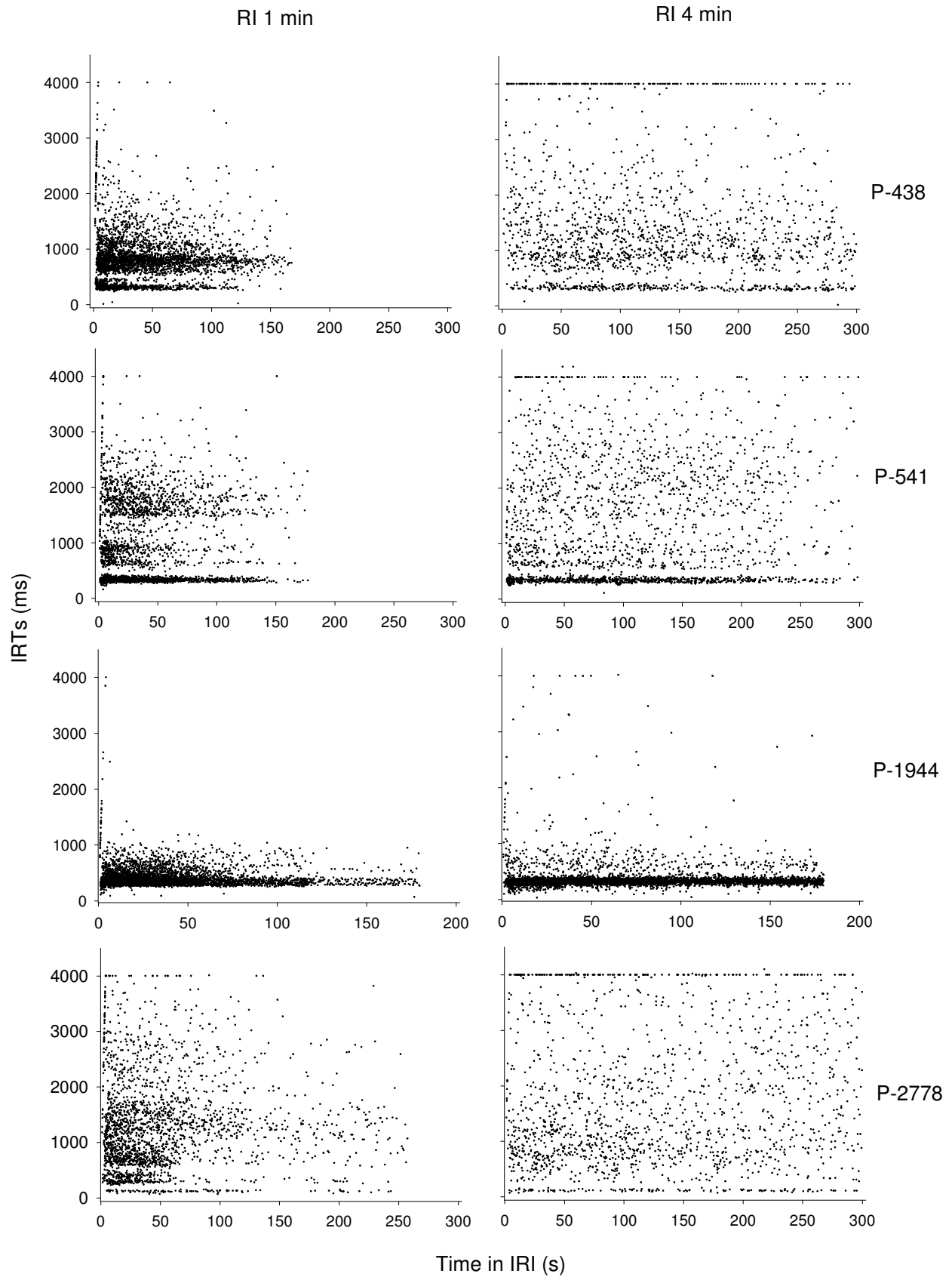
Fig. 7. Log-survivor plots for each bird during control conditions. Log proportion of IRTs greater than some time are plotted as a function of elapsed time. Large dots represent the RI 1-min component and smaller dots represent the RI 4-component.

proportion of IRTs > 5 s and no IRTs > 10 s in length occurred during the rich component for each subject, while the lean component produced a greater proportion of each of these classes of IRTs. Almost all of P-1944's IRTs were less than 2 s during both components of the multiple schedule.

Figure 8 shows IRT plots as described by Palya (1992) for each pigeon. Rows show data for each pigeon and the left- and right-hand columns show data for the RI 1-min and RI4-min components, respectively. Each point on these graphs represents an individual IRT, its position on the y-axis representing the value of the IRT and its position on the x-axis indicating the IRT's temporal position during the IRI. Since there were relatively few long IRTs (> 4000 ms) and these IRTs did not show any clear patterns of responding, all IRTs in this class are represented as 4000 ms on the y-axis at the top of the graphs. These plots show a clear tendency for each pigeon to respond at certain IRTs, as indicated by the appearance of dark bands of responding across the IRI (see Palya, 1992). P-438 showed clear bands of recurrent responding at 350 ms and 700 ms during the rich component and a slight cluster of recurrent IRTs at 1050 ms. There were few IRTs in the 2000-4000 ms range and almost none at 4000 ms and above. During the lean component, a clear, but less prevalent, band was evident at 350 ms and a broader, more diffuse, band around 1000 ms was also present. There was an increase in the frequency of IRTs between 2000 ms and 4000 ms and the frequency of 4000+ ms IRTs, relative to the RI 1-min component.

P-541 showed a clear band of responding at 350 ms and 2 less prevalent bands of IRTs at approximately 700 ms and 1800 ms. As with P-438, there were few IRTs in the 2000-4000 ms range and almost none greater than 4000 ms in the rich component. Responding during the lean component also looked similar to that of P-438, with a clear band at 350 ms. The IRTs between

Fig. 8. IRT plots for each bird during control conditions. Individual IRT duration plotted as a function of time in the IRI. Data from the RI 1-min component are presented down the left-hand column and data from the RI 4-min component are presented down the right-hand column.



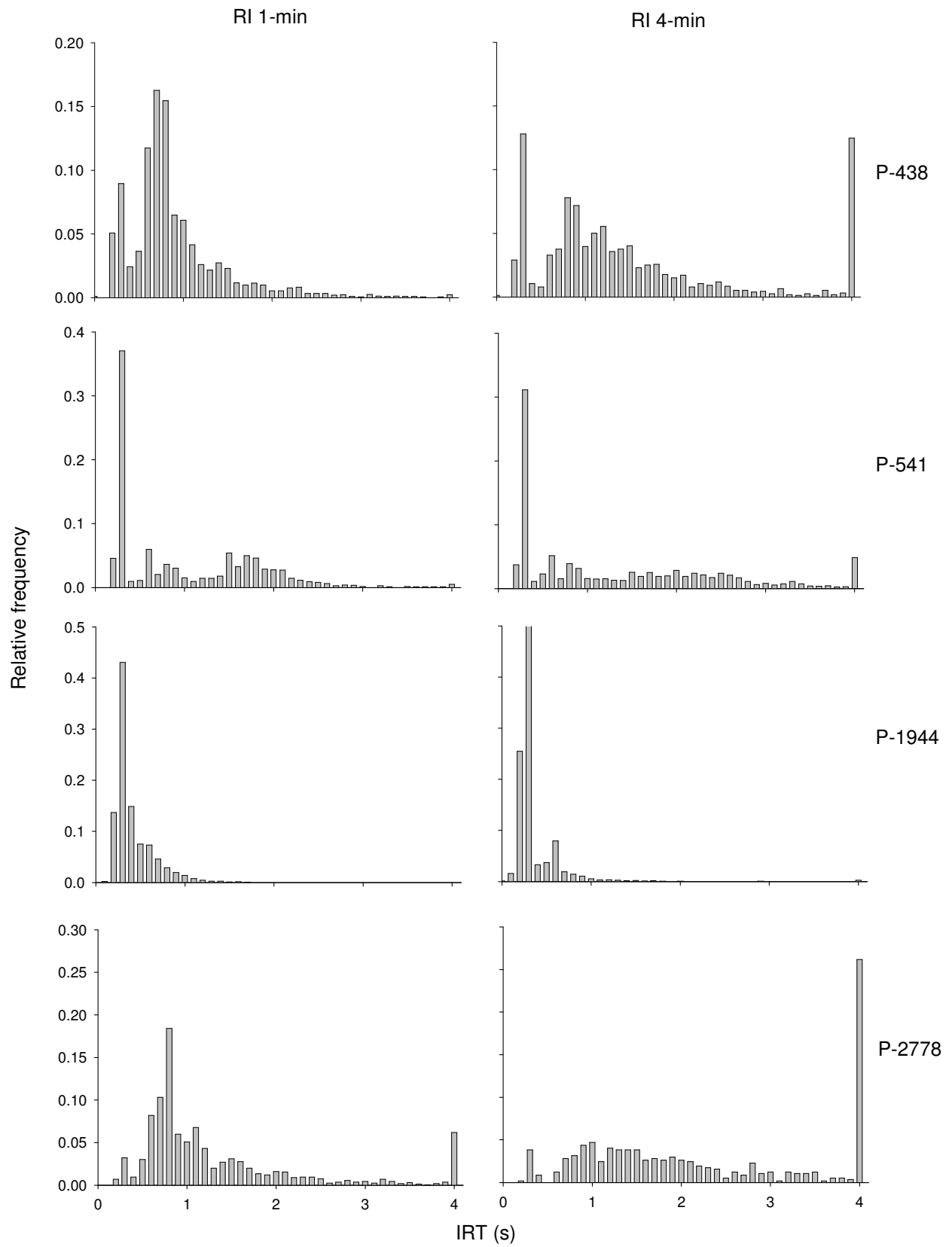
350 ms and 4000 ms showed no clear bands and there was an increase in the frequency of IRTs longer than 4000 ms, relative to those in the rich component.

P-1944, during the RI 1-min component, showed a clear band of responding at 350 ms and little responding at IRTs of greater length. Very few IRTs greater than 4000 ms were present. Responding during the RI 4-min component looked similar to that of the RI 1-min component. A clear band was evident at 350 ms with little (though more, relative to the RI 1-min component) responding at IRTs between 350 ms and 4000 ms. Slightly more IRTs longer than 4000 ms were present, compared with the RI 1-min component.

P-2778 showed clear bands of responding at approximately 150 ms, 350 ms and 700 ms during the RI 1-min component. Another, less prevalent band was apparent at 1400 ms in this component. The IRTs between 1400 ms and 4000 ms in length were present but did not cluster around a specific value. Few IRTs longer than 4000 ms were present during the RI 1-min component. Responding during the RI 4-min component showed a clear band at 150 ms. Other than a slight, diffuse band of IRTs around 1000 ms, responding between 150 ms and 4000 ms did not cluster around a single IRT value and the frequency of 4000+ ms IRTs was greater than during the RI 4-min component.

Relative frequency plots for both components during control are shown in Figure 9 for each bird. These plots graph the relative frequency of IRTs (number of IRTs during a given bin/total number of IRTs) in 0.1 s bins. Responding for P-438 was clearly multimodal in nature with peaks occurring in the 0.2-0.3 s bins and a second mode beginning at approximately 0.6 s. Compared with the RI 1-min component, fewer IRTs were included in this second mode, and there were increased instances of moderate length (2 – 4 s) and the longest IRTs (> 4 s) during the RI 4-min component.

Fig. 9. Relative frequency graphs for each bird during control conditions. Relative frequency of IRTs is plotted as a function of IRTs in 0.1s bins. Data from the RI 1-min component are presented down the left-hand column and data from the RI 4-min component are presented down the right-hand column.



A substantial proportion of the IRTs for P-541 occurred in the 0.3 s bin with other peaks beginning at approximately 0.6 s and 1.5 s during the rich component. Few IRTs of moderate (2-4 s) or long (> 4 s) length occurred during this component. During the lean component, responding was organized in much the same way with fewer IRTs occurring during each of these modes and greater instances of both moderate and long IRTs than had occurred during the rich component.

The majority of P-1944's responding during both the rich and lean component was clustered in the 0.2-0.3 s bins with very little responding occurring beyond IRTs longer than 1 s. There was little change between these two components, with a slight tendency to respond at more frequently at shorter IRTs during the lean schedule.

A small peak in the distribution of IRTs occurred in the 0.3 s bins during both RI 1-min and RI 4-min components for P-2778. A second and more prominent peak occurred beginning at approximately 0.6 s in the RI 1-min component. Fewer IRTs of moderate length (2-4 s) occurred during the RI 1-min component, relative to the RI 4-min component and there was a greater relative frequency of longer IRTs (> 4 s) in the RI 4-min component.

Effects of Methamphetamine

Figure 10 shows dose-response functions for each pigeon. Overall rate of responding (responses per minute) is presented as a function of dose for each subject. Data points represent averages of control (C), saline (S) and drug sessions. Rates during the RI 1-min components are represented by filled circles and rates during RI 4-min are represented by filled triangles. Error bars are constructed from the range of rates obtained under each condition. Three of the subjects acquired the discrimination and responded more frequently during the rich component under control and saline conditions. P-1944's response rates under both control and saline were

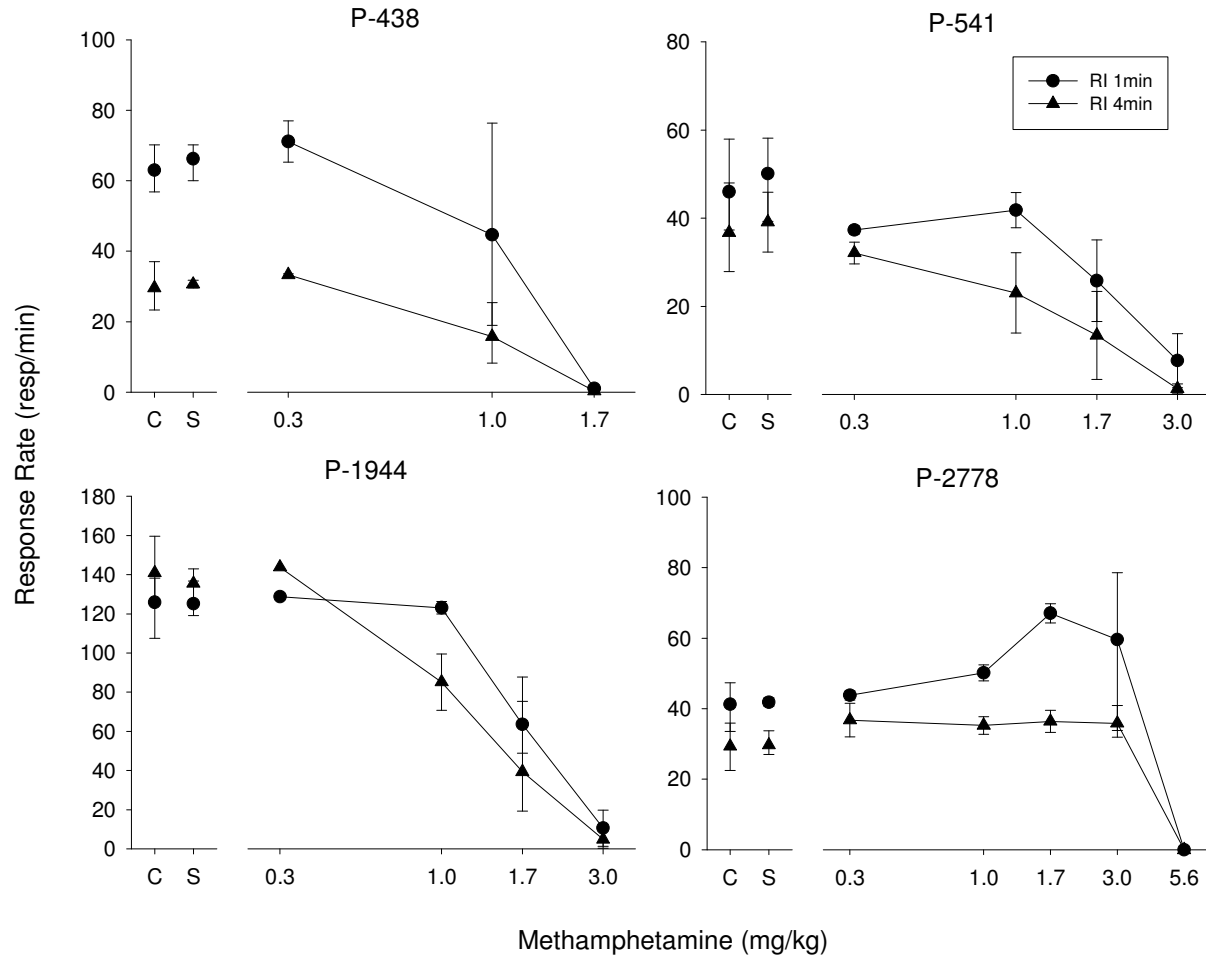
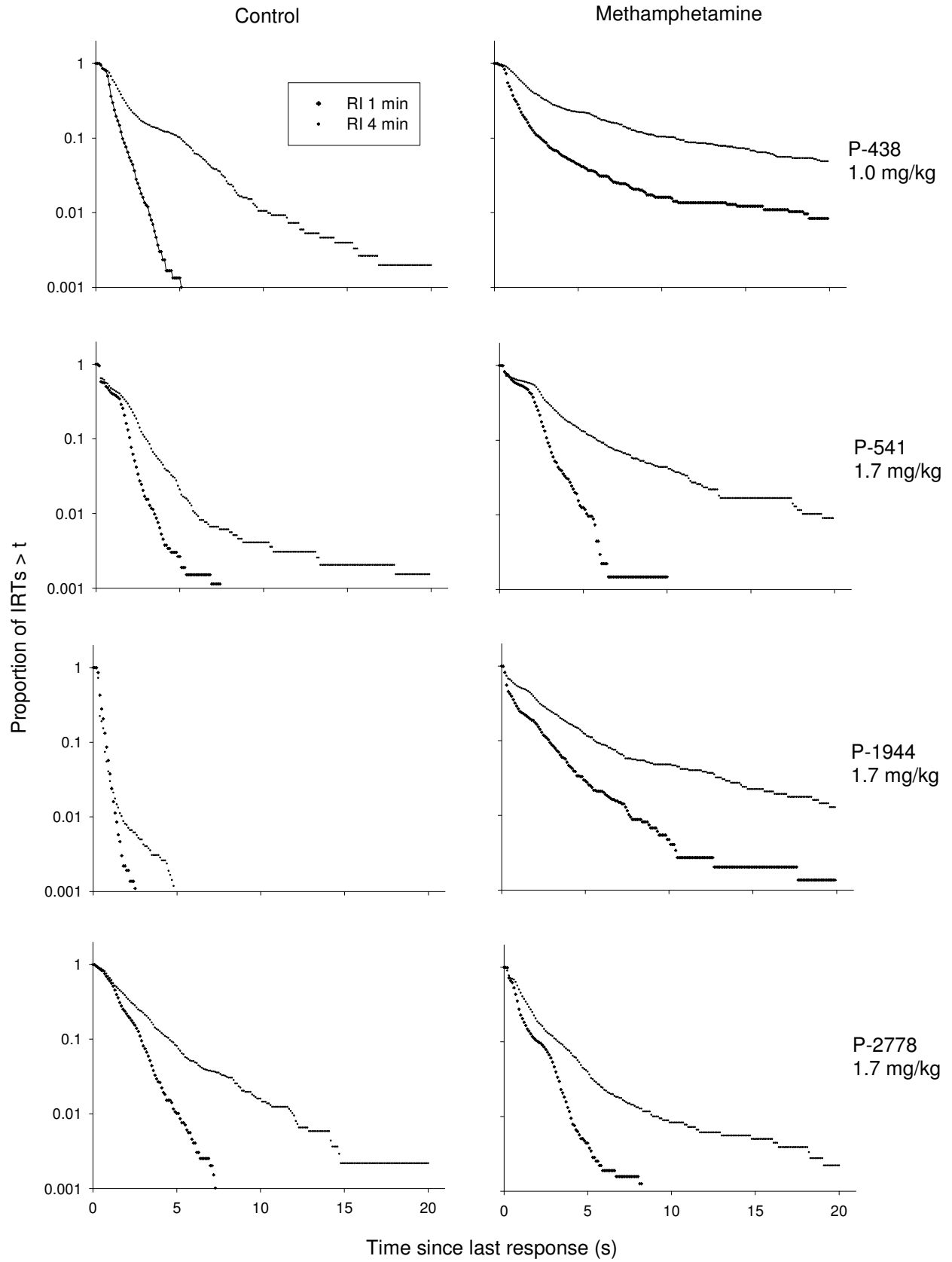


Fig. 10. Dose-response curves for all subjects. Rate of responding is plotted as a function of control, saline and drug sessions. Closed circles represent response rates during RI 1-min and closed triangles represent rates during RI 4-min.

similarly high in both components. For three of the subjects (P-438, P-541, and P-1944), there was a dose-related decrease in overall rate of responding. For these pigeons, intermediate doses (1.0 and/or 1.7 mg/kg) tended to produce a greater rate decrease under the lean component than under the rich component. Note that, as stated earlier, overall response rates for P-1944 were similarly high during both components. Responding during the RI 4-min component was disrupted slightly more by the administration of methamphetamine than was responding during the RI 1-min component, as indicated by the greater slope for this function. P-2778 showed a dose-related increase in responding during the RI 1-min component up to 3.0 mg/kg methamphetamine and essentially no change in rate during the RI 4-min component; 5.6 mg/kg eliminated responding in both components.

Figure 11 shows log-survivor plots during rich and lean components during both control and drug conditions. Figures in the left-hand column represent control data for each of the 4 subjects and figures in the right-hand column show log-survivor plots when each pigeon was administered a dose of methamphetamine. Doses of methamphetamine which produced moderate effects on response rates (1.0 mg/kg for P-438; 1.7 mg/kg for P-541, P-1944 and P-2778) were chosen for analysis in each of these plots. Responding during the rich component is represented by larger dots and responding during the lean component is represented by smaller dots. As during control conditions (left), no evidence of a “broken-stick” pattern was seen when methamphetamine was administered (right). Multiple breaks were seen in several of these plots (P-541, P-2778 and faintly in P-1944) under drug conditions. Also, there tended to be similarities between the RI 1-min and RI 4-min components in the initial 1 s of the functions and then a difference in slope during the later IRTs – a characteristic which was also observed in the control log-survivor functions. In most of these drug plots (all birds during RI 4-min and P-2778 during

Fig. 11. Log-survivor functions for all birds during control and at either 1.0 or 1.7 mg/kg. Control data are presented down the left-hand column for comparison. Log proportion of IRTs are plotted as a function of elapsed time. Large dots represent the RI 1-min component and smaller dots represent the RI 4-component.



RI 1-min), there was a smooth transition from short to long IRTs instead of a clear broken-stick function. That is, there seemed to be evidence of at least two states occurring, but not a sharp discrimination between these two states. With the exception of the data shown for P-2778, methamphetamine produced an upward shift in each function similar to the shift produced by varying the amount or rate of reinforcement (Shull et al., 2001). P-438, when given drug, showed a decrease in the slopes of these survivor functions during both components and the evidence of multiple breaks that was seen during control performance was not apparent. These survivor functions appeared somewhat similar to those found with nose-poking in rats.

The overall pattern of responding was similar under both control and methamphetamine conditions for P-541. These survivor functions each show the multiple breaks described earlier, and it appears that these functions are shifted upward over the whole range of the survivor plots. As in control conditions, the functions look similar at the shortest IRTs and pull apart at the longer ones.

The greatest effect on the survivor functions was seen in P-1944. This subject produced very steep functions with very few IRTs longer than 1 s in both components under control conditions. When administered 1.7 mg/kg methamphetamine, these functions were shifted upward and a number of IRTs beyond 1 s in length were emitted.

P-2778, whose rates of responding during the RI 1-min component increased when administered 1.7 mg/kg, showed a pattern of responding that was similar to that of control performance in other birds (multiple-break patterning). The slopes of these functions during drug were increased as a result of the higher rates of responding and fewer IRTs (relative to control conditions) of longer length.

Figures 12-15 show IRT plots during control and methamphetamine conditions for each pigeon. In each of these figures, control data are represented in the left-hand column and drug data are represented in the right-hand column. Data from the RI 1-min component are shown in the top row and data from the RI 4-min component are shown in the bottom row of each figure.

Figure 12 shows IRT plots for P-438 during control and at 1.0 mg/kg. This dose tended to reduce the pronounced appearance of IRTs around 350 ms, 700 ms and 1050 ms during the rich component. This dose also increased the tendency for responding to occur at both moderate (2000-4000 ms) and longer IRTs (> 4000 ms) in this component. This dose also decreased the occurrence of IRTs at 350 ms and around 1000 ms during the RI 4-min component and had only slight effects on IRTs longer in length.

Figure 13 shows IRT plots for P-541 during control and at 1.7 mg/kg. The effects of this dose for P-541 were similar to those for P-438 in that it tended to reduce the appearance of bands at 350 ms and 700 ms in the rich component; it also decreased the occurrence of IRTs at a band around 1800 ms. There was also a slight increase in the number of IRTs of moderate duration (2000-4000 ms) and those greater than 4000 ms. Methamphetamine decreased the prominence of the bands around 350 ms and 700 ms during the lean component, practically eliminating the band at 700 ms. IRTs residing above these bands (1000-4000 ms) were decreased in number and IRTs of longer duration (> 4000 ms) were increased in number during the lean component.

Figure 14 shows IRT plots for P-1944 during control and at 1.7 mg/kg. This dose tended to decrease the appearance of the band of IRTs at 350 ms and increase the frequency of all IRTs longer than 350 ms during the RI 1-min component. This dose of methamphetamine had a

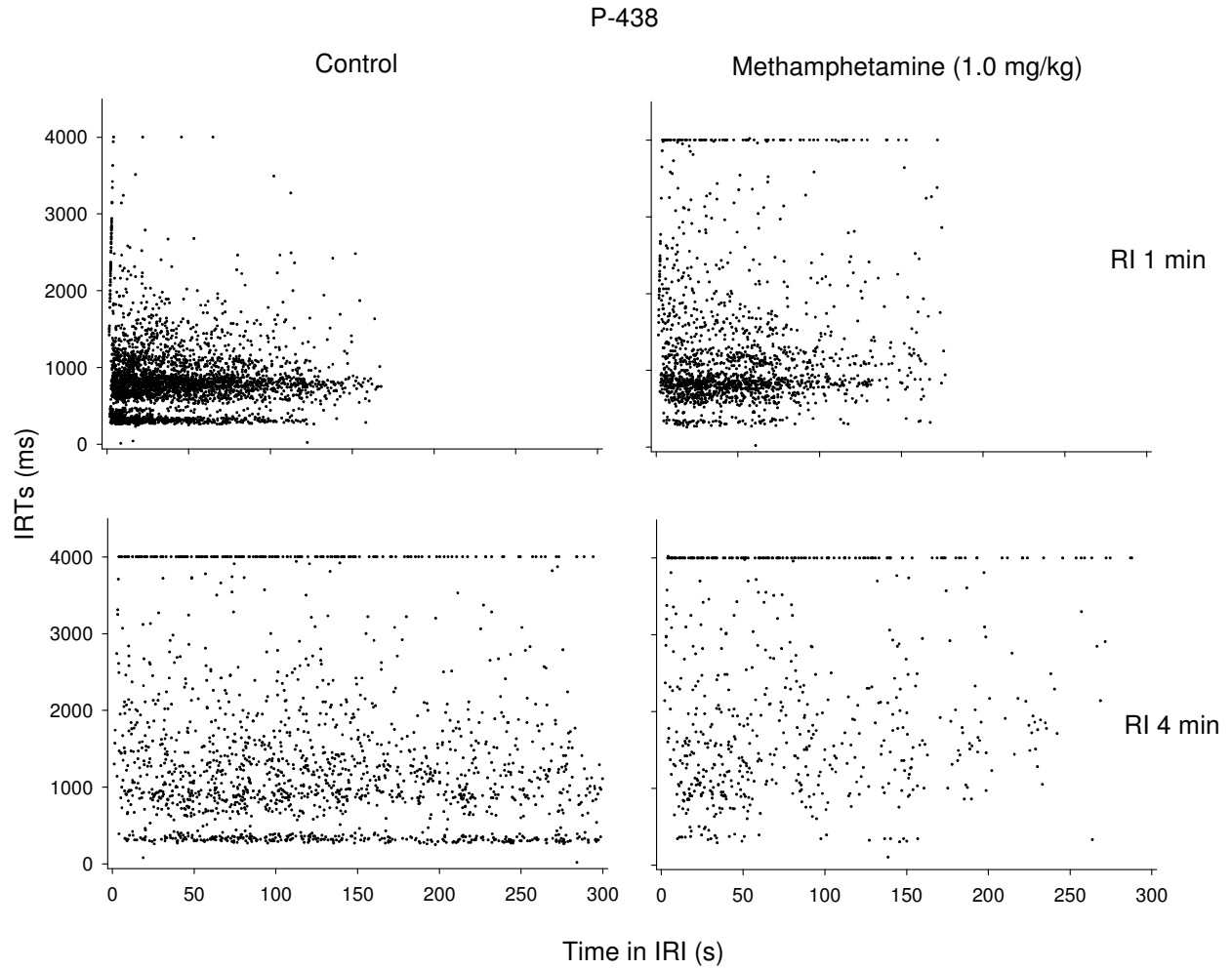


Fig. 12. IRT plots for P-438 during control and at 1.0 mg/kg. Control data are presented down the left-hand column for comparison. Individual IRT values are plotted as a function of time in the IRI. The top row represents data from the RI 1-min component and the bottom row represents data from the RI 4-min component.

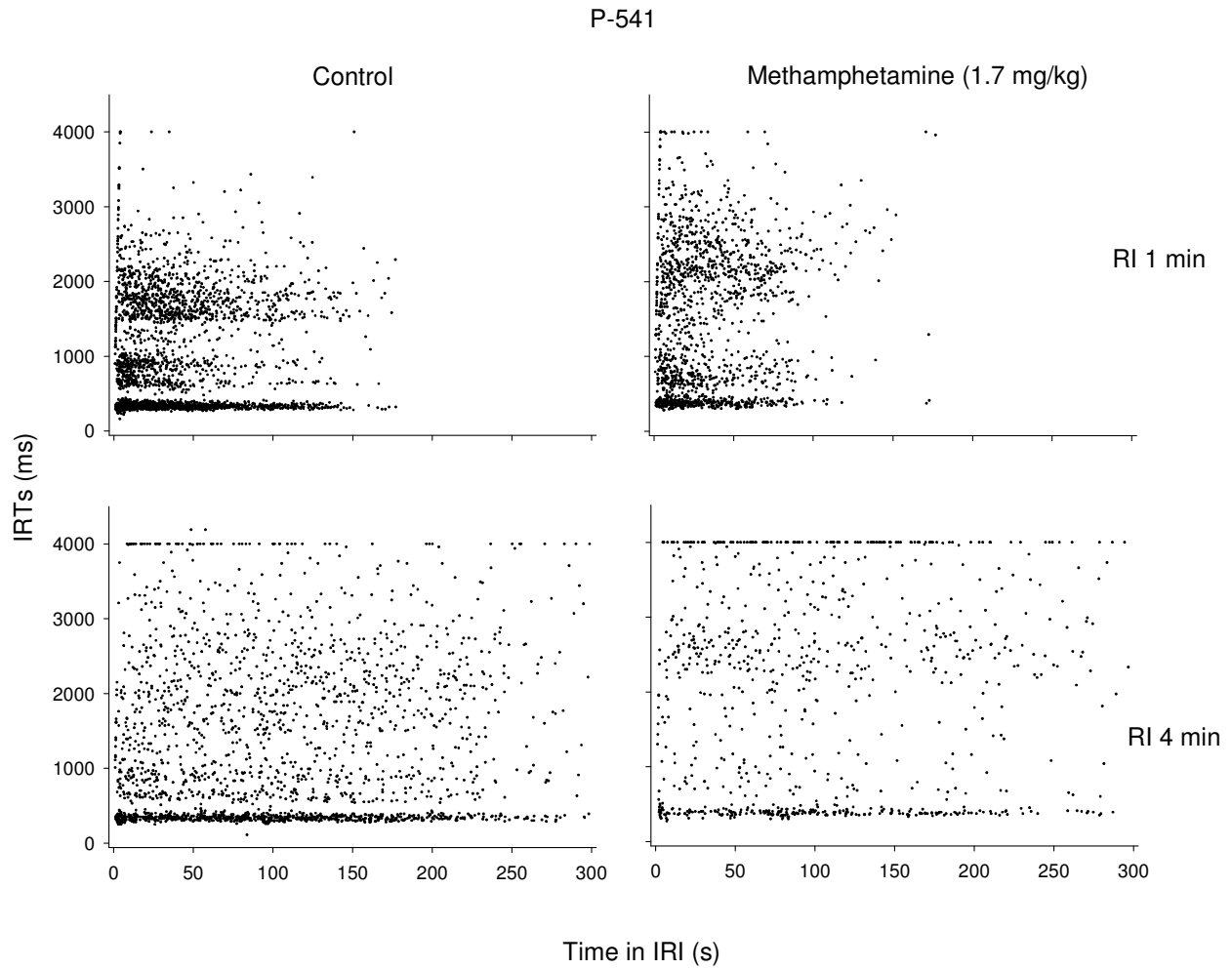


Fig. 13. IRT plots for P-541 during control and at 1.7 mg/kg. Control data are presented down the left-hand column for comparison. Individual IRT values are plotted as a function of time in the IRI. The top row represents data from the RI 1-min component and the bottom row represents data from the RI 4-min component.

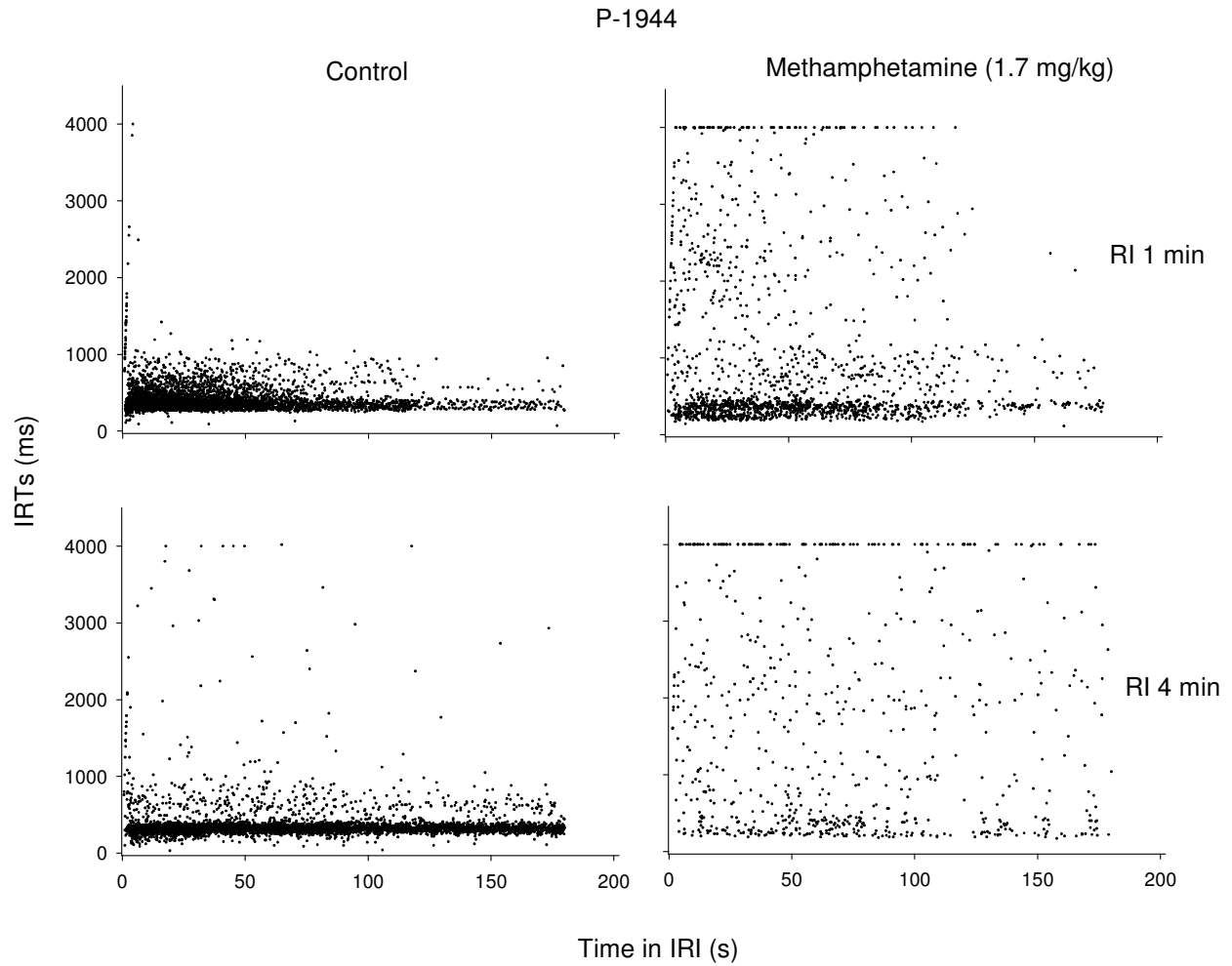


Fig. 14. IRT plots for P-1944 during control and at 1.7 mg/kg. Control data are presented down the left-hand column for comparison. Individual IRT values are plotted as a function of time in the IRI. The top row represents data from the RI 1-min component and the bottom row represents data from the RI 4-min component.

similar effect on responding during the RI 4-min component, reducing the frequency of IRTs at the 350 ms band and increasing the frequency of all IRTs longer than 350 ms.

Figure 15 shows IRT plots for P-2778 during control and at 1.7 mg/kg. It is important to note that, in contrast with the reduction in rates of behavior seen in other subjects, this dose of methamphetamine increased response rate during the rich component and had little effect during the lean component. Methamphetamine had little effect on the occurrence of IRTs in the band at 150 ms, but increased the occurrence of IRTs around 350 ms, 700 ms and 1400 ms. The frequencies of both IRTs of moderate length (2000-4000 ms) and those of longer length (> 4000 ms) were unaffected during the rich component. During the lean component, this dose of methamphetamine appeared to increase the occurrence of IRTs at 150 ms, 350 ms and 700 ms slightly but had little effect on IRTs above these bands (> 1000 ms). It is interesting to note that, though there was slight evidence that the general structure seen in the plots of other subjects was present during control conditions, the administration of this dose of methamphetamine tended to make this structure more pronounced.

The plots in Figures 12-15 appear to show differential effects of methamphetamine on different classes of IRTs. Figures 16-19 provide a more explicit analysis of this possibility. These figures show relative frequency plots for each bird during both control and drug conditions (1.0mg/kg for P-438; 1.7mg/kg for P-541, P-1944, and P-2778). Control data are presented on the left-hand side for comparison and drug data are presented on the right-hand side of the graphs. These plots graph the relative frequency of IRTs in each 0.1 s bin (number of IRTs during a given bin/total number of IRTs). If methamphetamine affected all IRTs equally, the shapes and frequency of IRTs during these distributions should be the same for both control and methamphetamine conditions, but the distributions would be shifted to the right and left when

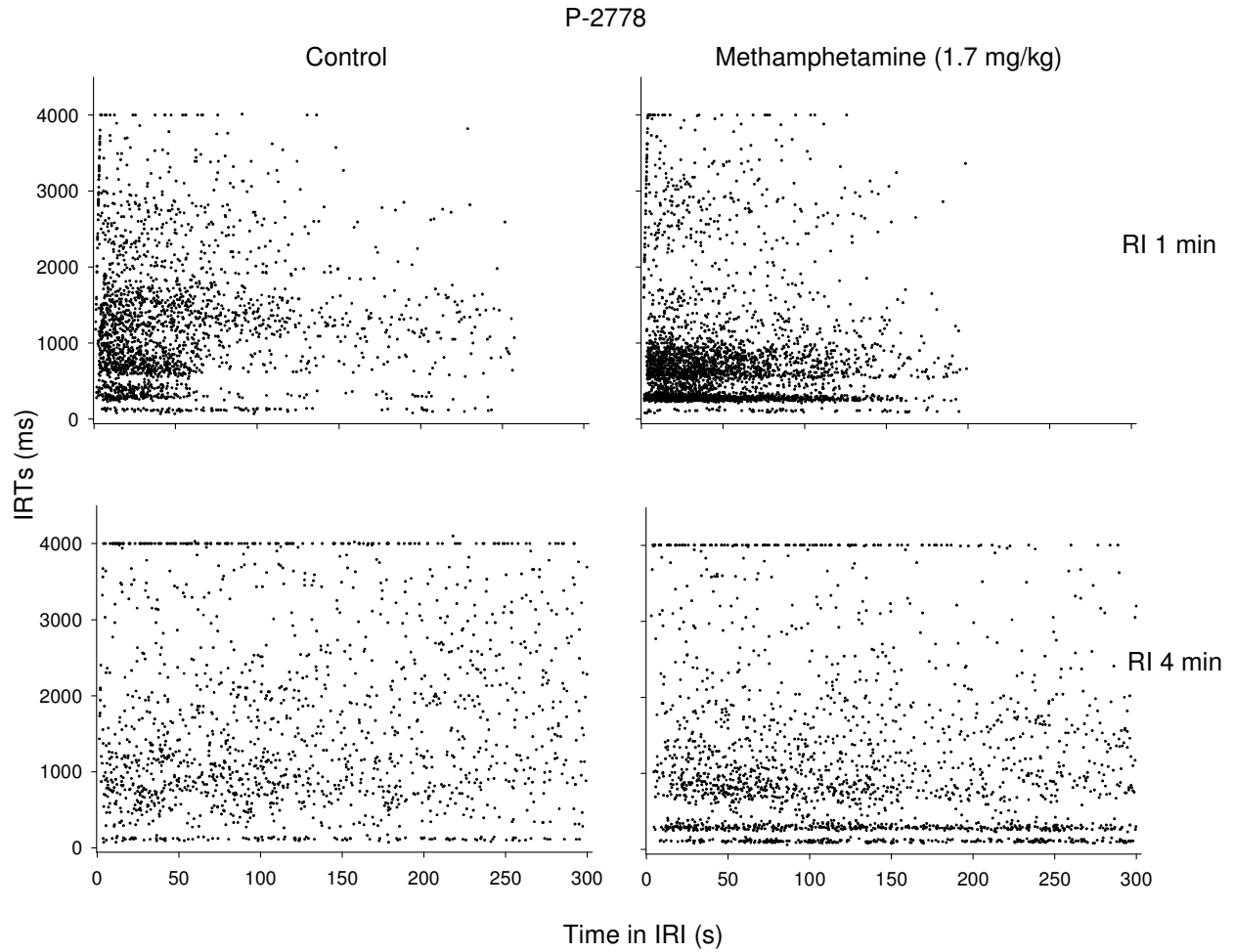


Fig. 15. IRT plots for P-2778 during control and at 1.7 mg/kg. Control data are presented down the left-hand column for comparison. Individual IRT values are plotted as a function of time in the IRI. The top row represents data from the RI 1-min component and the bottom row represents data from the RI 4-min component.

response rates were decreased and increased, respectively. For P-438 (Figure 16), the shapes of the distributions for both RI 1-min and RI 4-min components were similar during control and drug conditions. When methamphetamine was administered, there was a reduction in the frequency of very short IRTs (0.2 – 0.3 s) during both components. Also evident were slight increases in the relative frequency of IRTs of moderate length (2-4 s) and a larger increase in the frequency of very long IRTs (IRTs > 4 s) during both components.

Relative frequency graphs for P-541 are presented in Figure 17. Most of the effect on this subject's overall rate of responding in both components was due to a decrease in the frequency of very short IRTs (0.2-0.3 s) when methamphetamine was administered. Also evident was a slight increase in the frequency of moderate-length IRTs (2-3 s) and an increase in the frequency of the longest IRTs (> 4 s) in both RI 1-min and RI 4-min.

For P-1944 (Figure 18), most responding occurred during the first few bins of IRTs (almost all was contained within the first second) and was therefore most affected by methamphetamine. Again, IRTs within these first few bins (0.2-0.3 s) decreased with administration in both components. IRTs longer than 1s increased in frequency as did the frequency of the longest IRTs (> 4 s) during both components.

Relative frequency plots for P-2778 are presented in Figure 19. Methamphetamine increased the frequency of very short IRTs (0.2-0.3 s) and reduced the relative frequency of longer IRTs (> 4 s) during both components. These relative frequency plots suggest that, though control distributions were different for each bird, the effects seen on overall rates of responding by the administration of methamphetamine were mainly produced by an decrease in the frequency of short IRTs, an increase in the frequency of long IRTs, and an increase in the spread of the distribution for P-438, P-541 and P-1944. For P-2778, effects of methamphetamine were

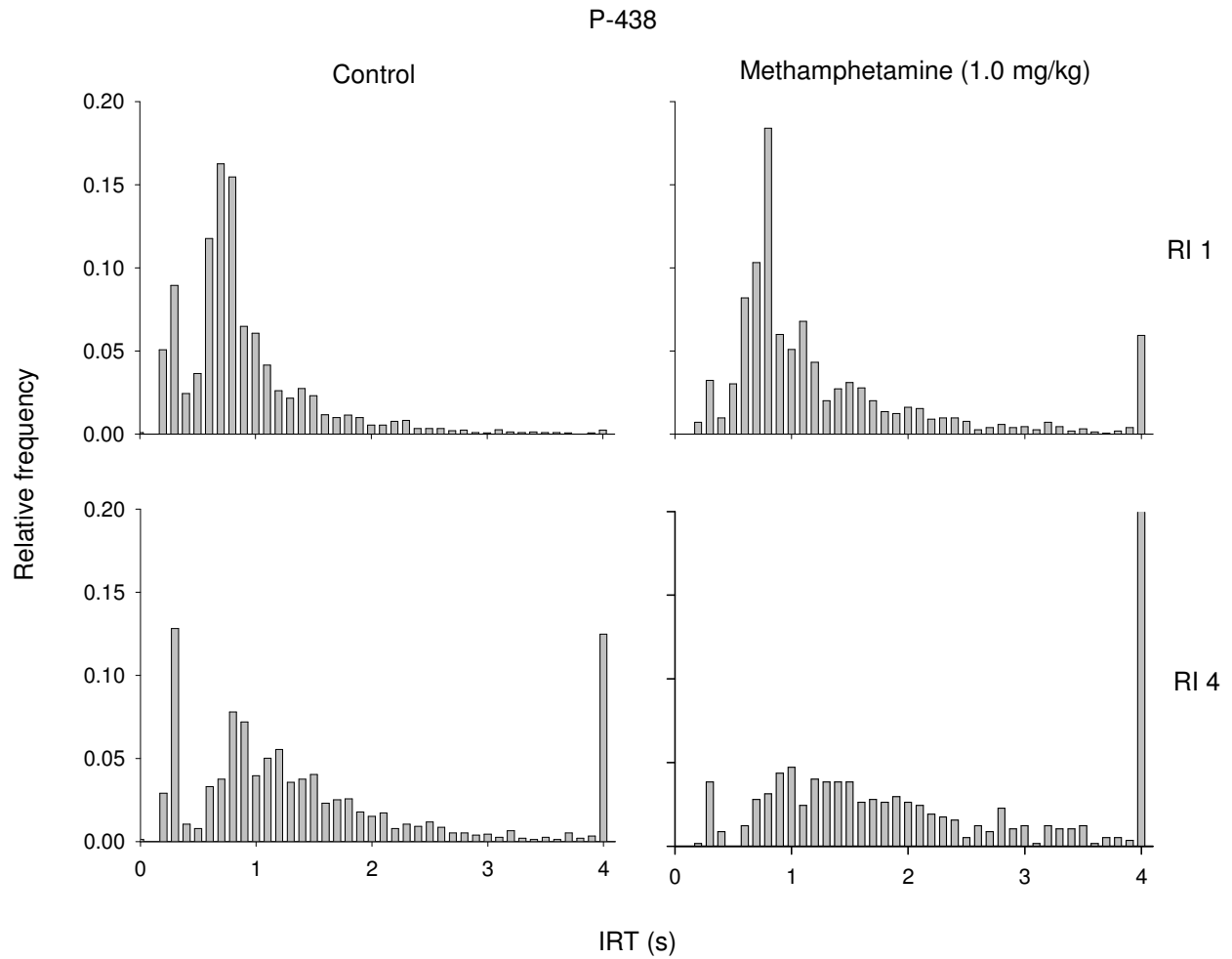


Fig. 16. Relative frequency graphs for P-438 during control and at 1.0 mg/kg. Control data are presented down the right-hand column for comparison. Relative frequency of IRTs is plotted as a function of IRTs in 0.1s bins.

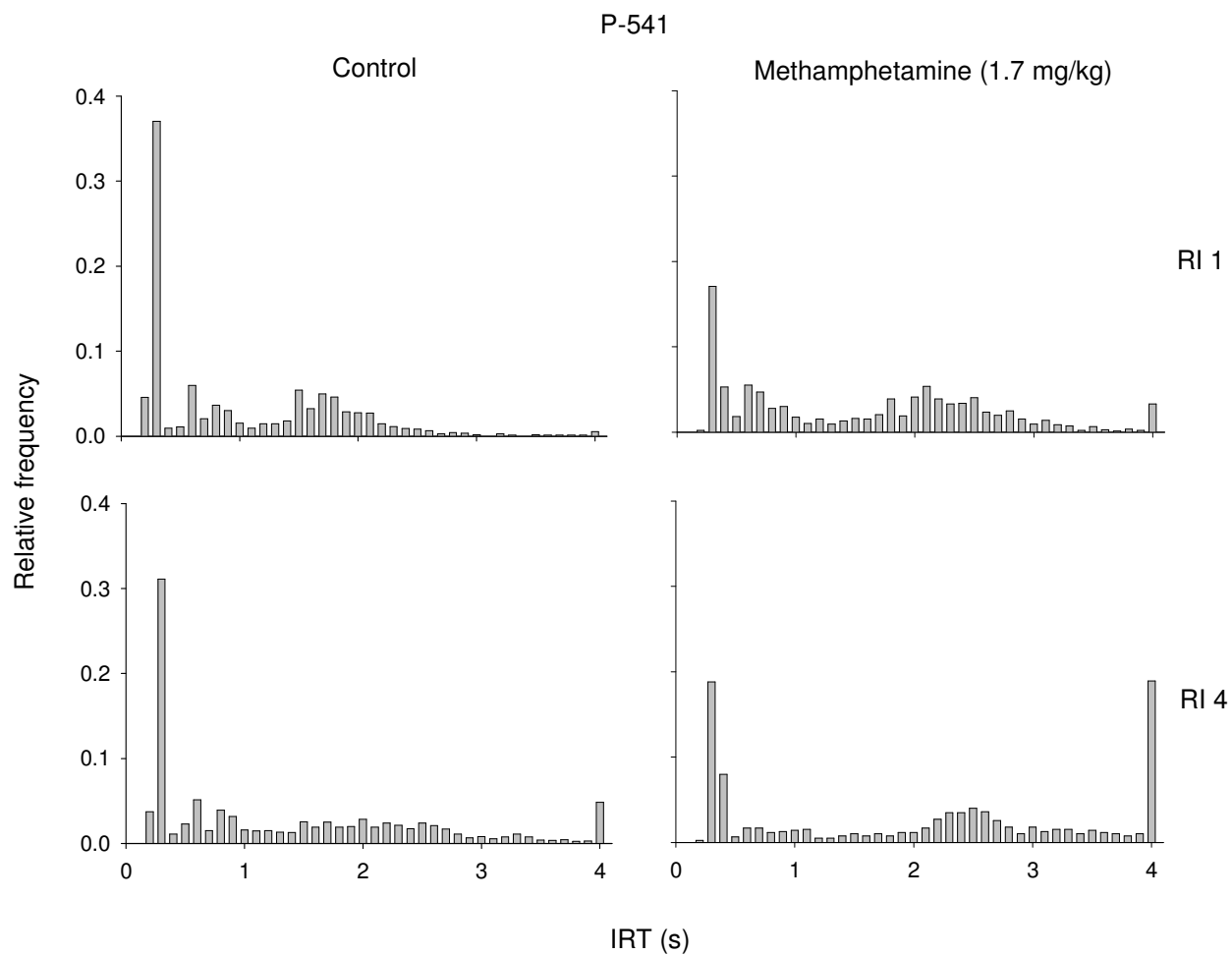


Fig. 17. Relative frequency graphs for P-541 during control and at 1.7 mg/kg. Control data are presented down the right-hand column for comparison. Relative frequency of IRTs is plotted as a function of IRTs in 0.1s bins.

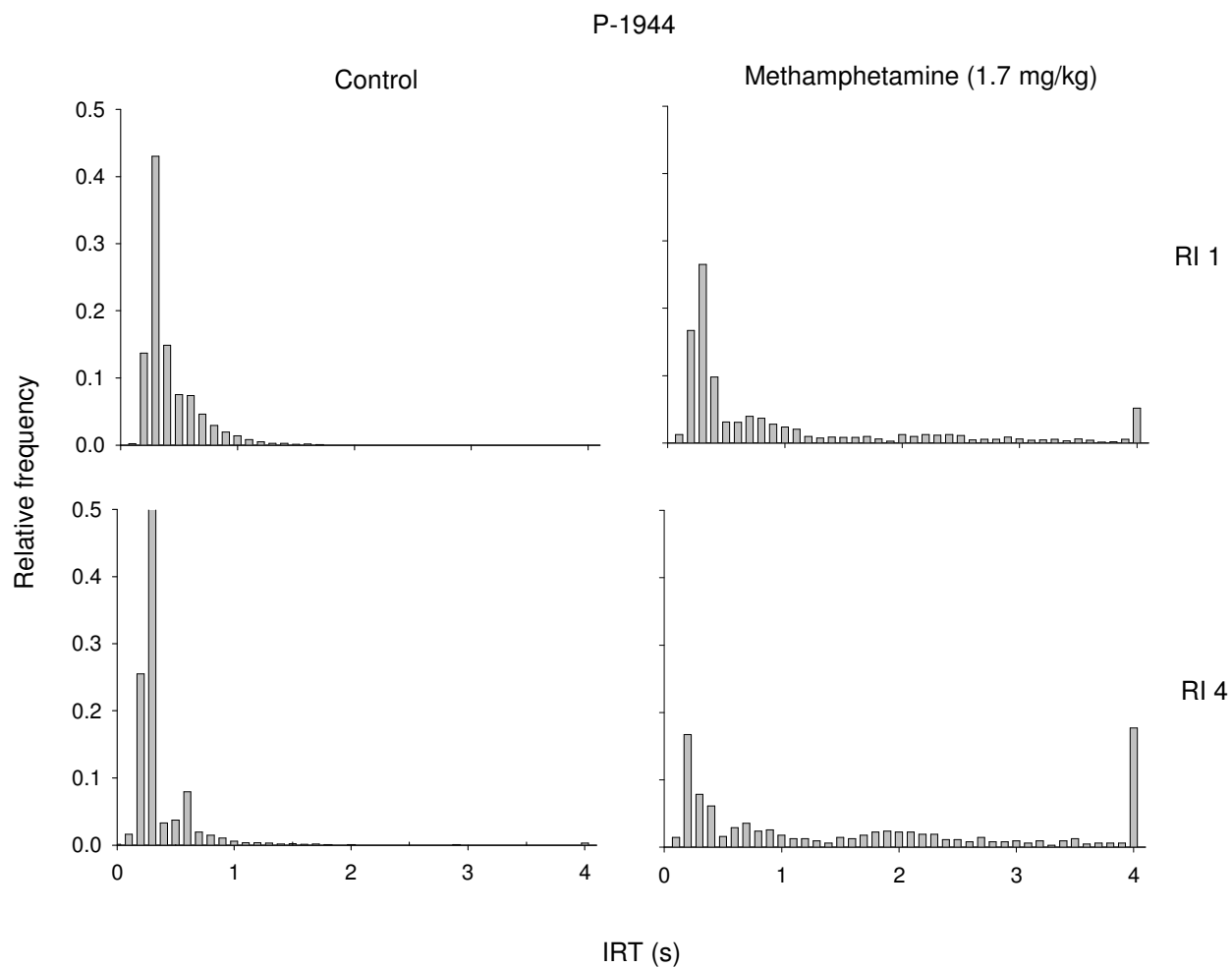


Fig. 18. Relative frequency graphs for P-1944 during control and at 1.7 mg/kg. Control data are presented down the right-hand column for comparison. Relative frequency of IRTs is plotted as a function of IRTs in 0.1s bins.

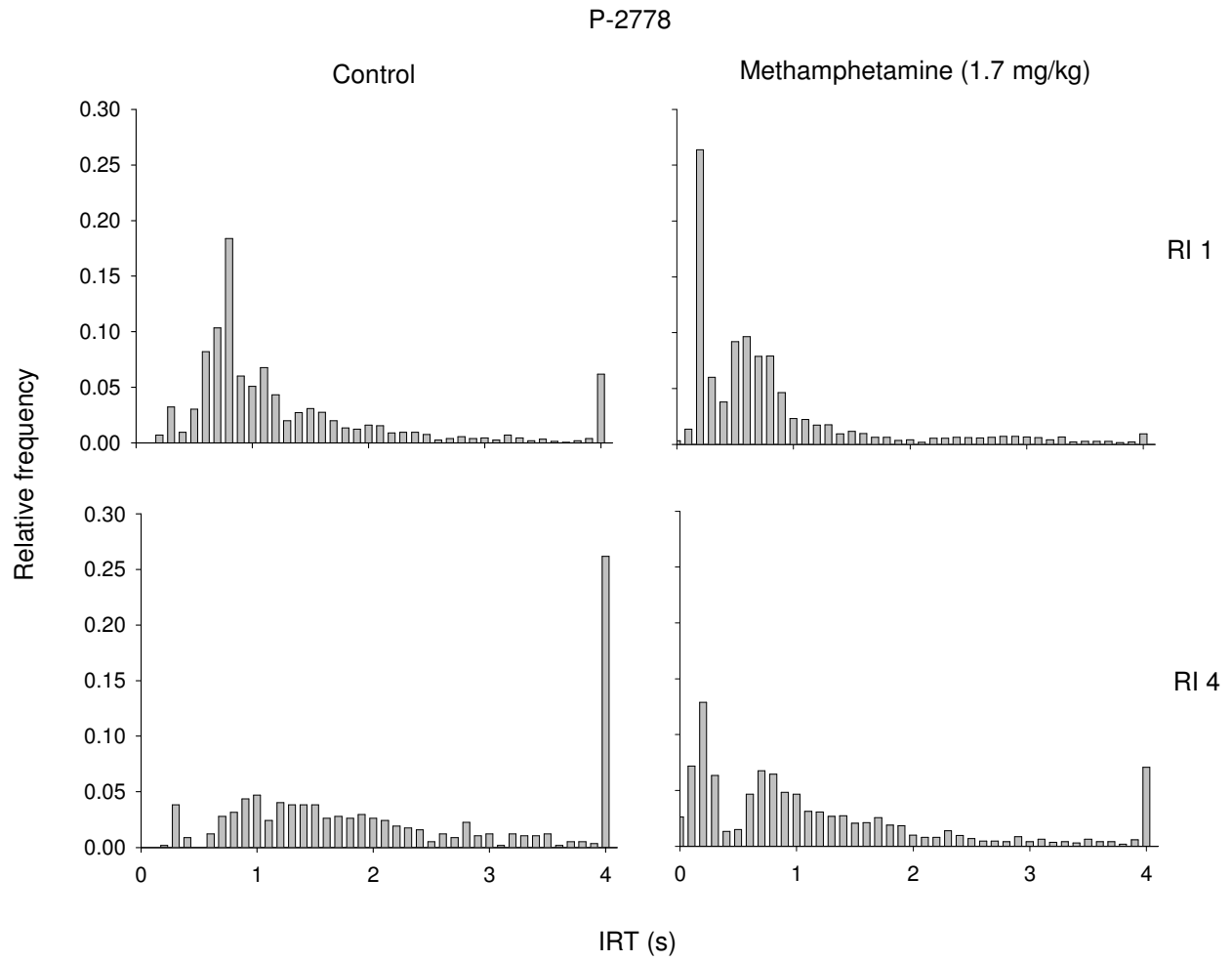


Fig. 19. Relative frequency graphs for P-2778 during control and at 1.7 mg/kg. Control data are presented down the right-hand column for comparison. Relative frequency of IRTs is plotted as a function of IRTs in 0.1s bins.

produced by an increase in the frequency of short IRTs and a decrease in the frequency of longer IRTs.

Summary

Log-survivor analyses showed no clear evidence of the broken-stick patterning observed in previous studies with rats (Shull et al, 2001) and some of these functions showed multiple breaks in early IRTs (> 1 s). Administration of moderate doses of methamphetamine tended to shift the control survivor functions upward in a manner similar to that of altering the schedule value in previous studies (Shull et al, 2001). The IRT and relative frequency plots revealed more evidence of the organization of pigeon responding on random-interval schedules. These plots suggested that responding was recurrent in nature and centered on IRTs of specific values (e.g., 350 ms and 700 ms). These recurrent IRTs (and IRTs > 4000 ms) were most affected by administration of moderate doses of methamphetamine, whether overall response rates were increased or decreased.

DISCUSSION

Control Performance

Log-survivor plots did not show the clear “broken-stick” pattern obtained in previous studies (Shull et al, 2001; 2002, 2004). As a result, it was impossible to fit functions to these data in order to obtain estimates of bout initiation rate and/or number of responses within a bout. Previous studies were conducted with rats and either nose-pokes or lever-presses. Thus, the log-survivor analysis may not extend to pigeon key-peck responding, at least not under the conditions of the current experiment. Although small breaks were evident in some of the

survivor plots, suggesting some tendency for responses to be clustered around multiple IRTs, these functions did not reveal clear evidence of a two-state characterization of responding.

It is unclear whether the log-survivor functions of the present study show what might be conceptualized as bout initiations, responding within a bout, some combination of the two, or some other type(s) of responding. As a result of the shift upward in the survivor functions during the lean component compared to the rich component, one might speculate that responding in the present study was mainly comprised of bout initiations. Recall that any change in the slope of the right-hand limb of a typical “broken-stick” function was the result of differences in the rate or amount of reinforcement in previous studies (e.g., Shull et al., 2001). In the current results, we would expect to see this shift upward, as the rates of reinforcement varied between the two components. In accordance with findings by Shull et al. for the right-hand limb, the entire survivor functions during the rich alternative in the present study had a greater slope than did those during the lean alternative. Subjects tended to emit a greater proportion of short IRTs and fewer IRTs of longer length during the rich component than during the lean component. Davison (2004) reviewed several studies of concurrent VI performance and found the opposite effect – slopes during components with higher rates of reinforcement tended to be less than those during components with lower rates of reinforcement. However, a reasonable explanation is available for these results: with concurrent schedules, relatively less time is spent during components with the lean rates of reinforcement and therefore, fewer opportunities for IRTs of long length (those which have the greatest effect on the latter portions of the limb) are available.

Another characteristic observed in some of the survivor plots of the present study was the multiple small breaks occurring at the very short IRTs. These multiple-break patterns have been observed previously in a review of concurrent schedule literature conducted by Davison (2004).

Davison constructed log-survivor plots by graphing IRTs from several studies using concurrent schedules and pigeons. When survivor functions were analyzed, several showed a multiple-break pattern similar to that observed in the current study (e.g., Figure 7: P-438 and P-541). Davison suggested the possibility that more than two processes are operating in pigeon responding in these cases, thus resulting in a series of breaks as opposed to the single clear break observed in the log-survivor functions of rat nose-poke behavior. It is necessary to consider, according to Davison, that responses other than key-pecks (scratching, moving about the chamber, pecking not directed at keys, etc.) are variable in nature. Davison thus suggests that a single between-bout time is improbable and that the multiple-breaks seen in pigeon survivor functions are a result of these varying durations of between-bout activities.

The log-survivor analysis described by Shull et al. (2001) did not extend to pigeon key-peck responding and, therefore, apparently did not provide a useful method to analyze the effects of methamphetamine under the current experimental preparation. Perhaps key-pecking in pigeons is a mixture of respondent *and* operant behaviors and cannot be separated by a two-state process model – pigeons peck naturally in order to obtain food and thus, some respondent properties of responding may be occurring as well. Brown and Jenkins (1968) followed key-light illumination with response-independent hopper presentations and showed that pigeons reliably pecked the response key after varying numbers of pairings, even when key lights were not centered above the hopper. This phenomenon, known as “autoshaping,” has been documented in numerous other studies (e.g., Williams and Williams, 1969; Perkins, Beavers, Hancock, Hemmendinger, Hemmendinger and Ricci, 1975) and has even been shown, though responding was not maintained, when presentations of inaccessible grain followed key-light illumination (Zentall and Hogan, 1975). That pigeon key-pecking is so easily acquired, even in the presence

of response-independent food presentation, suggests the possibility that some respondent properties are present within what we consider to be an operant. Although some of the key pecks in the current study may have been respondent, it is unclear which IRT class(es) contained such responses. . An interesting test to this hypothesis would be the replication of this experiment with pigeons and some other response topography, such as a treadle-press, which is less likely to have respondent properties. The importance of this analysis would be emphasized if pigeon treadle-press responding revealed the broken-stick functions seen with rats in the log-survivor plots. Drug effects could then be studied using this analysis and motoric effects potentially could be separated from those on reinforcer efficacy.

Another possibility for the lack of a broken-stick function is that the noise in these graphs is great enough (that is, the two distributions overlap by a considerable amount) that it is virtually impossible to determine if responding is composed of mainly bout initiations or within-bout responses. In order to determine if the broken-stick functions can be produced via behavioral manipulation without the use of an entirely different response, one might add a small VR requirement to the end of the RI schedules in effect. Presuming pigeon key pecking conforms to the same principles as rat nose poking, this would emphasize the initial portion of the log-survivor function. Shull et al. (2001) showed that changing the schedule of reinforcement from a standard VI schedule to a tandem VI VR resulted mainly in a change in the number of responses per bout. Perhaps this manipulation would emphasize the within-bout responses and separate the IRT distributions enough to produce the broken-stick function seen in previous studies.

Another possible reason for the lack of replication of Shull's (2001) results is that the RI schedule values used in the current study did not provide low enough rates of reinforcement to

reveal a two-state distribution of pigeon key-peck responding. It is well known that the sensitivity of response rate to the changes in rates of reinforcement is hyperbolic in nature – that is, as the rate of reinforcement increases, the response rate becomes less sensitive to these changes as it reaches its maximum rate. Herrnstein (1970) provided us with the equation:

$$B = kR / (R + R_0) \quad (1)$$

where B is the rate of responding, R is the rate of reinforcement and k and R_0 are parameters obtained from fitting a curve to the data and represent the asymptotic response rate, and the rate of reinforcement that produces a response rate equal to half its asymptote, respectively. The R_0 parameter has been interpreted as the rate of alternative, unscheduled reinforcement. Shull (2005) analyzed results from a number of pigeon and rat studies which incorporated VI schedules and examined the values of R_0 obtained in each study. Shull noted that increasing reinforcer rate above that indicated by the value of R_0 can produce, at most, just a twofold increase in response rate. Therefore, increases in reinforcement rate under these conditions, even by as much as tenfold, can do nothing more than merely double the rate of responding.

In light of this evidence, it would benefit researchers interested in the effects of reinforcement rate on behavior to include rates of reinforcement that are below the values of R_0 . Shull (2005), however, noted that obtained values for R_0 in pigeon studies have frequently been less than those for rats and that studies with pigeons often did not include reinforcement rates that were below the obtained values for R_0 . The rates of reinforcement in the present study (rich:60/hour & lean:15/hour) were above the average R_0 Shull reported for pigeons. Therefore, the current experiment should be replicated with lower reinforcer rates.

Essentially, then, the current study and those reviewed by Shull (2005) with pigeons were conducted in a lean environment with relatively low rates of alternative reinforcement in

comparison to studies with rats. With such low rates of extraneous reinforcement, the probability of a two-state process occurring may be very low – if the pigeon obtains a relatively low rate and/or small amount of reinforcement from alternative sources, it is less likely to sample from those sources for extended periods of time and therefore enter a longer period of between-bout responding. This is consistent with the interpretation that most of the responding contained in the pigeon survivor plots is that of bout initiations which was arrived at as a result of the change in slope over most of the function with changes in reinforcer rate. If the pigeon is sampling alternative reinforcement at frequent and short periods, initiation rates would be high with very short periods between response bouts. Manipulations which would affect the value of R_0 (reductions in rate of reinforcement, decreased deprivation levels, shorter hopper durations or administration of amphetamine (Heyman, 1983) would be of interest in further studies if this interpretation is true and the rate of bout initiations is indeed high in the current study. Another manipulation which has been shown to increase the values of R_0 is to introduce some form of extraneous reinforcement into the chamber during an experimental session. Petry and Heyman (1997) studied rat responding on a number of VI schedules of varying rates and attempted to manipulate values of R_0 by introducing cardboard tubes into the chambers. These tubes effectively increased values of R_0 and left estimates of k unchanged. These manipulations, all of which serve to increase the values of extraneous reinforcement, may cause pigeons to respond more in a bout like pattern – engaging in longer-lasting alternative behaviors and thus increasing the duration of between-bout intervals.

The IRT plots in the current study indicated a clear tendency for pigeons to respond at 350 ms and often at multiples of 350 ms throughout the IRI, a result which is in line with those from several other studies (Blough, 1963; Blough & Blough, 1968, Palya, 1992) under various

schedules of reinforcement. Blough (1963) suggested that these IRTs occurring at multiples of the main band might be the result of a failure of clear pecks to strike the key. This failure would result in additional bands of responding at multiples of the main band (or what might be called “harmonics”). Responding beyond these bands (IRTs > 1 s) tended to not cluster around any single IRT value and resembled the pattern of responding observed by Blough when he noted that the relatively even spread of responses beyond this band was evidence of the response independence of these IRTs. In some cases (e.g., P-2778) there was a band of IRTs (at approximately 150 ms) that was below the main band. Similar results were reported by Blough and Blough (1968). They suggested that these pecks essentially were “double peck units” (p 25) and were the result of pigeons effectively making a response in such a manner that the key would be operated twice within a normal peck IRT of 350 ms. In support of this theory, Blough and Blough noted that a study by Shimp (1967) did not find these same bands of IRTs when using keys which required a force of 22 g to operate – in contrast with the 14 g of force required to operate the keys in their experiment. This additional force requirement could be enough to diminish the ability of a pigeon to operate the key multiple times within the time it would take to make a single peck. Weiss and Gott (1972) also noted the appearance of what they termed “nibbles” below the main band of clear key pecks and suggested that pigeons were performing this response by the quick opening and closing of their beak when centered close to the response key. Another plausible explanation for these very short IRTs is simple key-bounce – the subject pecks the key hard enough that it returns to its original state and then registers another peck via a bounce of the key. These bands of IRTs occurring below the main band have been shown to be relatively insensitive to changes in the schedules of reinforcement, but might be affected by manipulations which exert their effects by altering the organism’s ability to perform certain

responses. To the extent that the pigeon is still capable to perform the “nibble” response, an increased force requirement would separate these two explanations.

The relative frequency graphs for each pigeon provided more evidence of the multi-modal nature of responding observed in the present experiment. With the exception of P-2778, modes of responding were clearly evident around 350 ms (between 0.3 and 0.4 s) and again just below 1 s during the rich component. Few responses which ended long IRTs (> 4 s) occurred for these subjects. P-2778 showed no evidence of the mode around 350 ms seen in other birds' responding, and showed a clear spike in the distribution of IRTs beyond 4 s. During the lean component, a decrease in frequency around the mode beginning at 1 s and a clear increase in the occurrence of IRTs longer than 4 s was apparent for all birds except P-1944. These results were similar to those seen during the rich component. P-1944 showed a less pronounced spike in the distribution beyond 4 s. The second mode in each of these distributions occurred at approximate multiples of the main mode again, suggesting an organization of responding similar to that seen in previous studies (Weiss and Gott, 1972; Palya, 1992). The responses comprising the main mode may be considered clear pecks and those around the second mode in the distribution may be considered the harmonics mentioned earlier.

Previous studies (e.g., Branch and Gollub, 1974; Gentry et al., 1983) have suggested that the use of averages to describe the effects of manipulations on behavior can mask order which might be observed through the use of more detailed analyses. The data presented here add to this growing literature and indicate that microanalyses can reveal order at a more molecular level than is captured simply by presenting overall response rate within a session.

Effects of Methamphetamine

Administration of methamphetamine tended to shift the log-survivor functions upward, decreasing their slope. As discussed earlier, a reduction in slope of the right-hand limb of the survivor functions has been described as a change in the rate of bout initiations and has been produced by changes in the rate or amount of reinforcement provided by the schedule (Shull et al., 2001). However, as also mentioned earlier, without a clear broken-stick function, it was impossible to determine if bout initiation rate was the only type of responding affected by the administration of methamphetamine. One might speculate that, since methamphetamine tended to show effects similar to those between the rich and lean components in the current study (a general shift upward in the survivor functions), that methamphetamine acts to alter the reinforcing efficacy of food – the variable that has been implicated as affecting the initiation stems of the survivor analysis (Shull et al., 2001). This result would be in accord with results of a study by Heyman (1983) which used Herrnstein's (1970) hyperbolic equation to characterize the effects of *d*-amphetamine. Heyman noted that changes in *k* have been observed in studies which altered the response required to produce reinforcement (Herrnstein, 1974). Since R_0 is the rate of reinforcement which maintains half of the maximum rate of responding, this parameter is undoubtedly altered by manipulations which alter reinforcer efficacy. Rats were run on a five-component multiple schedule with differing VI values (VI 10 s – VI 160 s) in each component. Administration of *d*-amphetamine increased response rates, but served to only decrease R_0 and had no systematic effects on the parameter *k*. From these results, it was interpreted that *d*-amphetamine exerted its effects by mainly increasing the efficacy of reinforcement. Methamphetamine in the current study had the opposite effect (a decrease in response rates) in most cases, but this effect may be explained by results presented earlier (Shull, 2005). If pigeon

responding is already near asymptote in this study under control conditions, it is not likely that methamphetamine would be able to produce increases in response rates. Also, subjects in Heyman's study were rats and produced response rates that were lower than those presented here. Regardless, these findings with methamphetamine are consistent with the notion that responding in the log-survivor functions here was comprised mostly of bout initiations, as changes in the rate or amount of reinforcement (changes which would speak to the efficacy of reinforcers) tend to alter this measure of responding. However, as it is impossible here to rule out the presence of the within-bout limb, one cannot rule out the possibility that methamphetamine produced what could be considered a motoric effect in these plots.

With the exception of P-2778, methamphetamine tended to exert most of its effects by decreasing the prevalence of IRTs within the bands occurring in the IRT analysis described by Palya (1992) and, in some cases, increased the number of moderate-length IRTs throughout the IRI. Longer IRTs (> 4 s) were increased in frequency as well. It is interesting to note that, in the one subject which methamphetamine produced an increase in the rate of responding (P-2778), the administration of this drug tended to increase the density of these main bands of IRTs and made this subject's performance look similar to that of other subjects under control conditions. It was unclear from this analysis whether methamphetamine affected all IRTs equally regardless of length or if the effects of the drug were confined mainly to IRTs of certain length. In order to determine this, relative frequency distributions were plotted for each bird during conditions in which methamphetamine was administered.

The relative frequency plots suggested that IRTs were not affected equally. There was a clear tendency for methamphetamine to affect mainly those IRTs of shorter length (0.2-0.3s) with a slight affect on longer IRTs. Methamphetamine tended to decrease the occurrence of these

shorter IRTs while increasing the occurrence of longer IRTs in 3 of the 4 birds (P-438, P-541 and P-1944). Data from P-2778, whose response rates increased when administered methamphetamine, showed the opposite effect - a tendency for methamphetamine to increase the occurrence of shorter IRTs and decrease the occurrence of longer IRTs.

Three different types of responding (nibbles, clear pecks, and misses) were suggested by Weiss and Gott (1972) as comprising overall rate of pigeon key-peck behavior on FR schedules. Nibbles, clear pecks, and misses occurred at approximately 120 ms, 280 ms and 560 ms, respectively. The subjects in the present experiment produced IRTs clustering around the 350 ms mark, suggesting that, by this interpretation, most responding was comprised of clear pecks. If the IRTs within this band represented clear pecks to the key, then the effects of methamphetamine are in line with previous results. Weiss and Gott found that amphetamine tended to eliminate almost all instances of nibbles to the key, reduced the frequency of clear pecks, and increased the frequency of both harmonics (misses) and IRTs longer than 1 s. In the present study, methamphetamine tended to affect the frequency of IRTs clustered around 350 ms and the frequency of IRTs longer than 4 s. In order to confirm that the responding observed in this study is comprised of mostly clear pecks to the key, it would be interesting to use an increased force requirement for the pigeon key, as Shimp (1967) did. One might expect this manipulation to decrease the “nibbles” that are commonly reported and to have relatively little effect on the frequency of clear pecks and misses.

A number of studies have found that microanalyses have revealed orderly drug effects that were not otherwise apparent. For example, under concurrent schedules, Zirriax et al. (1993) found that, although d-amphetamine produced orderly effects on overall rates of responding and rates of switching, a microanalysis was required to reveal the mechanisms by which this order

was produced. Both switch rates and overall rates decreased in a dose-dependent fashion when *d*-amphetamine was administered. However, response rate decreases were the result of a shift from shorter IRTs to very long IRTs and switchrate decreases were the result of a the widening of the distribution of visit durations.

The doses of methamphetamine presented here produced either an increase or decrease in overall rates of responding. However, these summary measures did not provide information as to how these changes in rate occurred. Methamphetamine primarily affected shorter IRTs, but also affected IRTs of longer duration; intermediate-length IRTs were relatively unaffected. With the detailed analyses presented here, it is clear that all responses may not be equivalent (e.g., nibbles, pecks, and harmonics) and that methamphetamine does not have a blanket effect on all of these IRTs. An increase in our oft-used measure of overall response rate may be accounted for in a number of ways – by an increase in the tendency to emit shorter IRTs or a decrease in the tendency to emit longer IRTs. Shorter IRTs may be affected by manipulations which have no affect on longer IRTs, and vice versa. When one uses overall response rate as a measure of performance, the effect that a certain manipulation may have on these individual types of responding (IRTs) is obfuscated and, therefore, detailed analyses are an important tool for understanding the effects of drugs on operant responding.

Rate-dependency

A common interpretation of drug effects in the literature involves the idea of rate-dependency: that drug effects are dependent upon the control rate of responding engendered by the schedule of reinforcement. Sanger and Blackman (1975) found that response rates under VI schedules were affected differently by *d*-amphetamine than response rates under a paced VI schedule (which generated relatively low response rates). *d*-Amphetamine decreased rates during

the standard VI schedule and increased rates during the paced VI schedule, suggesting that control rate of responding (and not the schedule in effect) was responsible for drug effects. In a more detailed analysis, Sanger and Blackman showed that d-amphetamine shifted the moderate-length IRTs (> 5s) towards shorter IRTs (approximately 2.5-5s) in the paced VI schedule. However, since response rate seems to be a product of a number of simultaneous processes occurring during a session (see Weiss and Gott, 1972, Palya, 1992, Shull et al., 2001), the use of overall rate as a measure in order to describe the effects of drugs may obscure important order at a more molecular level.

Weiss and Gott (1972) used microanalyses to study the effects of several drugs on FR 30 performance and found all IRTs within the ratio were affected similarly by drug administration. Rate-dependent effects of drug administration were not apparent as drug affected all IRTs in the same manner – both those which might be considered low-rate (post-reinforcement time - PRT) and those which might be considered high-rate (all other IRTs). However, when studying IRT distributions, Weiss and Gott found that the reduced rate of responding observed when amphetamine was administered was a result of a combination effect on different types of IRTs (reduction in “nibbles” and clear pecks with an increase in the frequency of “harmonics,” which occurred as a result of pecks missing the key). Changes arising from the administration of amphetamine seemed to be changes in the response topography and not simply a change in the rate of output of behavior. Similar results were observed in the current study. While amphetamine showed a dose-dependent decrease in several of the birds’ overall response rates (P-438, P-541 and P-1944), IRTs of different durations were affected differentially by administration and thus, the effects of drug on responding during the current study might better be described as IRT-dependent. That is, IRTs of short length (approximately 350 ms) tended to

decrease in frequency with the administration of moderate doses of methamphetamine, while the occurrence of IRTs of longer length (> 1 s) tended to be increased when methamphetamine was administered, with the greatest increase in frequency being on those IRTs longest in length (> 4 s). In the one subject with increased rates of responding, these same classes IRTs were affected – the shortest IRTs were increased in frequency, and the longest IRTs were decreased in frequency. While this interpretation closely resembles rate-dependency (lower rates *were* increased while higher rates *were* decreased), it provides a more molecular approach to identifying the specific effects of drugs on behavior. It is important to notice that the data for 2778 were inconsistent with a typical rate-dependent account. For this bird, higher rates of responding (those responses ending short IRTs) were increased and lower rates (those ending longer IRTs) were decreased when methamphetamine was administered. Through more-detailed analyses, if pigeon responding is found to be comprised of formally different responses (e.g., nibbles vs. clean pecks), the behavioral effects of drugs might be better understood. Via molecular analyses, it may be possible to identify the variables which regulate the behavior more effectively, and to characterize the manner in which administration of a drug interacts with these variables. With results such as those reported by Weiss and Gott, and those presented here, it is not unreasonable to conclude that the effects of drugs might better be described as differential effects on different types (or topographies) of behavior instead of differential effects on different rates of behavior.

Summary

From the results of this study, it appears that the log-survivor analysis may not extend to pigeon key-pecking under random-interval schedules. However, as stated earlier, the analysis warrants further study to determine why this is not the case. The survivor functions, IRT plots,

and relative frequency analyses in the current study suggest that pigeon responding might be considered multi-modal in nature. Although they are unable to provide us with quantitative estimates of the different types of responding occurring within a session, the characteristics of responding seen in these analyses suggest that pigeon key-peck responding might be divided into component parts by alternative microscopic analyses. That similar recurrent responding was seen in previous studies regardless of the contingencies in effect and that bands also occurred at multiples of “clean-peck” IRTs in most schedules further suggests that vital information about the nature of responding is lost responding is aggregated across an entire session.

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