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BEHAVIORAL AND PHARMACOLOGICAL VARIABLES AFFECTING RISKY CHOICE IN RATS

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The effects of manipulations of response requirement, intertrial interval (ITI), and psychoactive drugs (ethanol, phencyclidine, and *d*-amphetamine) on lever choice under concurrent fixed-ratio schedules were investigated in rats. Responding on the ''certain'' lever produced three 45-mg pellets, whereas responding on the ''risky'' lever produced either 15 pellets ($p = .33$) or no pellets ($p = .67$). Rats earned all food during the session, which ended after 12 forced trials and 93 choice trials or 90 min, whichever occurred first. When the response requirement was increased from 1 to 16 and the ITI was 20 s, percentage of risky choice was inversely related to fixed-ratio value. When only a single response was required but the ITI was manipulated between 20 and 120 s (with maximum session duration held constant), percentage of risky choice was directly related to length of the ITI. The effects of the drugs were investigated first at an ITI of 20 s, when risky choice was low for most rats, and then at an ITI of 80 s, when risky choice was higher for most rats. Ethanol usually decreased risky choice. Phencyclidine did not usually affect risky choice when the ITI was 20 s but decreased it in half the rats when the ITI was 80 s. For *d*-amphetamine, the effects appeared to be related to baseline probability of risky choice; that is, low probabilities were increased and high probabilities were decreased. Although increase in risky choice as a function of the ITI is at variance with previous ITI data, it is consistent with foraging data showing that risk aversion decreases as food availability decreases. The pharmacological manipulations showed that drug effects on risky choice may be influenced by the baseline probability of risky choice, just as drug effects can be a function of baseline response rate.

Key words: drug effects on risky choice, intertrial interval and risky choice, fixed-ratio schedule and risky choice, foraging, risk taking, lever press, rat

When choosing between two alternatives differing in amount and probability of reinforcement, an organism is said to be risk prone if it prefers a larger, probabilistic reinforcer and risk averse if it prefers a smaller, certain reinforcer (Mazur, 1988). According to risk-sensitive foraging theories, a major, perhaps the most important, determinant of risky choice is reinforcer availability (Mazur, 1988). In particular, under conditions in which reinforcement is plentiful, risk-sensitive foraging theories predict that animals should be risk averse. Under conditions in which reinforcement is scarce, animals should be risk prone. For the most part, animal research that has studied the effects of the daily energy budget rule has supported this prediction when amount of food available from each source was manipulated (Kacelnik & Bateson, 1996), but studies of risky choice in birds have supported the prediction more consistently than have those in rats (review in Kacelnik & Bateson). Data inconsistent with the prediction were reported for rats by Hastjarjo, Silberberg, and Hursh (1990).

Hastjarjo et al. (1990) adapted the procedures used in studies of risk taking in humans, namely repeated-gambles experiments (Silberberg, Murray, Christensen, & Asano, 1988). Rats were presented with concurrent fixed-ratio (FR) 1 FR 1 schedules. They earned all of their daily food ration during the experimental session. In Experiment 1, each response on one lever produced three pellets and a response on the other lever produced either 15 pellets ($p = .33$) or no pellets ($p = .67$). Overall reinforcement was more plentiful for consistent responding on the

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risky lever, because the mean number of pellets available from the risky alternative was greater (five pellets per trial) than the number of pellets available from the certain alternative (three pellets per trial). To study the effects of reinforcer availability, Hastjarjo et al. manipulated the number of trials per session. As the number of trials per session decreased, the rats' choice behavior became more risk averse (i.e., they were less likely to choose the risky lever), and the rats lost weight. This result was not consistent with the prediction that animals should be risk prone when the available food supply is insufficient to meet caloric needs, and suggested that other variables may play a role in influencing risky choice. Hastjarjo et al. speculated that increased day-to-day variability in number of pellets earned when the number of trials per session decreased produced risk aversion, which overcame the risk proneness to be expected from the reduction in the total number of reinforcers received. In a second experiment, they held total trials per session and relative probability of reinforcement on the two levers constant but manipulated total amount of food available in each session. They found that risk aversion was inversely related to the total amount of food available.

The Hastjarjo et al. (1990) data exemplify a point made by Kacelnik and Bateson (1996), which is that the occurrence and direction of risk-sensitive choice can be influenced by apparently small changes in experimental procedures. Thus behavior generated under the procedure introduced by Hastjarjo et al. seemed likely to provide a sensitive baseline for studying other variables that might influence risky choice. We initially were interested in employing this behavioral baseline in the course of our behavioral pharmacology research to determine whether psychoactive drugs that have been considered to increase the probability of risky behavior in humans would increase the probability of risky choice in this rat model. After we failed to find changes in risky choice following drug administration, we made systematic behavioral manipulations with the hope of changing the baseline probability of risky choice. Because the results of the behavioral manipulations were themselves relevant to risk-sensitive foraging theory, we present the data first with respect to the behavioral manipulations and next with respect to the pharmacological manipulations conducted under different baseline conditions.

The first behavioral variable manipulated was response requirement under an FR schedule. When the animal has to do more work to obtain reinforcers (i.e., to obtain access to each "patch" in foraging terminology), it may be that food effectively becomes more scarce, which might decrease risk aversion. Previous research with birds that manipulated number of responses under concurrent schedules of reinforcement (i.e., not discrete-trials procedures) found behavior to be risk prone, regardless of response requirement (Ha, 1991; Ha, Lehner, & Farley, 1990).

The second behavioral variable manipulated was intertrial interval (ITI). Because we held session duration constant, increasing the ITI effectively decreased trials per session, as in Hastjarjo et al. (1990), but it also decreased reinforcement density (per unit time) and thus increased delay to reinforcement. Experiments that have manipulated variability in delay to reinforcement have found almost uniformly that animals showed risk-prone behavior (Kacelnik & Bateson, 1996). Kacelnik and Bateson's analysis of the contribution of various time components of a laboratory model of foraging suggested to them that delay to reinforcement once the response requirement has been met is a greater determinant of the effect of variability in delay to reinforcer delivery than is ITI. Few studies have manipulated ITI systematically, however, and none appear to have done so in the rat (see review by Kacelnik & Bateson).

In the pharmacological manipulations, we investigated the effects of the sedative drug ethanol, the dissociative anesthetic phencyclidine (PCP), and the stimulant *d*-amphetamine, all of which have been considered to promote risk-taking behavior under some circumstances in humans (Goodman, Rall, Nies, & Taylor, 1990). The effects of these drugs on schedule-controlled responding in rats and other species have been studied extensively (Dews & Wenger, 1977; McMillan & Leander, 1976) but, to our knowledge, they have not been studied on behavior generated under a risky choice procedure. Dose–effect relations were studied during two ITI conditions, 20 and 80 s, which produced lower and

higher probabilities of risky choice, respectively, in most rats.

METHOD

Subjects

Six experimentally naive, Long-Evans hooded male rats (Harlan Sprague-Dawley), received at 6 weeks of age, served as subjects. They were housed individually under a 12:12 hr nonreversed light/dark cycle with continuous access to water and with food freely available. At the beginning of habituation to the chambers, weights ranged from 241 to 279 g. Feeding was restricted during shaping of the lever press, but weight gain still was permitted. By the beginning of the risky choice procedure itself, weights ranged from 324 to 347 g, which is near the range (330 to 340 g) at which we typically maintain body weights for adult male rats of this strain during behavioral studies (Ator, 1991). Under the risky choice procedure, rats earned all food (45-mg Noyes Precision rat pellets) during the experimental sessions. When sessions were not conducted, the rats were fed 15 g of commercial laboratory rat chow, which typically results in weight stability or weight gain on the day the rat next is weighed.

Apparatus

Six experimental chambers (27.7 cm by 30.3 cm by 53.2 cm) were used, and each rat was assigned to one of the chambers for the duration of the study. The apparatus is shown in Ator (1991, p. 29). Two Gerbrands rodent levers (G6312) were mounted 13 cm apart and 5 cm above the floor; identically colored jewel lights were mounted 5 cm above the levers, one over each. A food cup was centered on the opposite wall 2.5 cm above the floor, into which a Gerbrands pellet feeder (G5100) delivered the 45-mg food pellets. The experimental enclosure was housed inside a larger sound-attenuating chamber. A ventilation fan and white noise, delivered through a speaker in the enclosure, masked extraneous sounds. Experimental control and data collection were accomplished via an IBM-compatible 386SX microcomputer programmed in the MedState Notation Language and interfaced to the chamber with Med Associates solid state components.

Procedure

After pressing both levers was shaped using the method of successive approximations, experimental sessions for all 6 rats were conducted at the same time of the afternoon Monday through Friday. The rats were placed in the experimental chambers for a 10-min presession timeout during which the chamber was dark and responses on the levers had no effect. At the end of the presession timeout, the light over one lever was illuminated and the first of 12 forced-choice trials began. During forced-choice trials, only a response (FR 1) on the lever below the illuminated jewel light could produce food pellets. For each rat, one lever was designated the certain lever and the other lever the risky lever. A response on the certain lever always produced three pellets, and a response on the risky lever produced either 15 pellets (p = .33) or no pellets (p = .67). The response turned off the jewel light and initiated the delivery of food pellets, at a rate of 1 per second, if they were available on that trial. Responses on the other lever had no consequence but were counted. A 20-s ITI began following the delivery of the last pellet or following the response if no pellet was scheduled to be delivered on that trial. During the ITI, the jewel lights were dark; responses on the levers had no effect but were counted. In the forced-choice trials, the probability of a risky trial or a certain trial was .5, with the restriction that six trials had to be with the risky lever and six with the certain lever. The subsequent trials all were free-choice trials, on which the jewel lights above both levers were lit and a concurrent FR 1 FR 1 schedule was in effect. The session ended after 93 free-choice trials or 90 min, whichever occurred first.

Before the first experimental manipulation, 20 baseline sessions were conducted. The first manipulation was to reverse the contingencies across the two levers to determine whether each rat's preference for either the risky or the certain contingency would track the change in lever assignment. After there were no increasing or decreasing trends in percentage of risky choice for at least five sessions, the contingencies again were reversed. The other experimental manipulations were carried out in the following order: effects of

drugs at ITI 20 s; FR manipulations; ITI manipulations; effects of drugs at ITI 80 s. The behavioral manipulations are grouped together first and the pharamacological second, however, for ease of presentation and discussion.

FR manipulations. To investigate the effects of work requirement, the FR values for both levers were increased in tandem across sessions. All rats were exposed to FR values of 1, 2, 8, and 16, in ascending order, followed by replication of FR 1 and then FR 16. Three of the 6 rats, which were ahead of the other 3 in moving through the conditions, also were exposed to FR 4 and FR 12; their data did not indicate value in studying FR 4 and 12 with the other rats. Each FR condition lasted for at least three sessions and until there were no increasing or decreasing trends in the percentage of trials on which the risky lever was chosen. The number of sessions until this criterion was met was usually three to six; at FR 2, it was seven for Rats 36-3 and 36-5 and nine for Rat 36-3. The median number of sesssions in the FR conditions was 4.5.

ITI manipulations. Following the FR manipulations, all rats were exposed to ITI lengths ranging from 20 s to 120 s in ascending order. Then the 20-s and the 80-s ITI conditions were replicated. Each ITI condition lasted at least three sessions and until there were no increasing or decreasing trends in the percentage of trials on which the risky lever was chosen. The number of sessions until this criterion was met in each ITI condition ranged from a low of 3, 4, or 5 to a high of 10, 11, 13, or 14, except that it was 7 to 16 for ITI 60 s and 8 to 18 for the replication of ITI 20 s. The median number of sessions in the ITI conditions was 7.5.

Pharmacological manipulations. Pharmacological manipulations were conducted under the concurrent FR 1 FR 1 condition at two ITI lengths (20 s and 80 s) to determine drug effects on different baseline rates of risky choice. Study of drug effects did not begin under either ITI condition until after at least 10 baseline sessions and no increasing or decreasing trend in percentage of risky choice over the last five. On test days, the drug was given and the rat was placed in the chamber for the presession period, which was lengthened or shortened to correspond to the interval desired between drug administration and the beginning of the session (see below). Drug testing occurred on Tuesdays and Fridays, provided that the percentage of risky choices in the preceding session fell within the range of percentages of risky choices in the last five sessions of the baseline before drug testing began, which usually occurred, so that testing did not have to be delayed. The order in which the drugs were studied during the 20-s ITI condition was ethanol, *d*-amphetamine, and PCP; during the 80-s ITI condition, it was *d*-amphetamine, PCP, and ethanol. Each dose usually was studied once in the 20-s ITI condition, because there was little general effect of the drugs. Doses often were repeated in the 80-s ITI condition because more effects were observed.

Ethanol was administered intragastrically 15 min before the session, by use of a curved 20-gauge, 3-in., 2.25-mm tip, stainless-steel feeding needle. An ethanol stock solution was prepared by adding distilled water to 95% weight/volume (w/v) ethanol (obtained from the Johns Hopkins Hospital pharmacy) to make a 15% w/v solution. Volumes of injection ranged between 1 and 5 ml, depending upon the amount needed to achieve the desired total dose. A 20% ethanol solution was used if the total volume of fluid would have exceeded 5 ml, which occurred for Rats 36-2 and 36-4 in the 20-s ITI condition and for Rat 36-6 in the 80-s ITI condition. Vehicle was injected at both 1- and 5-ml volumes in the 20-s ITI condition to control for the range of volumes of injection to which the rats might be exposed. Phencyclidine hydrochloride (National Institute on Drug Abuse) and *d*-amphetamine sulfate (Sigma) were administered by intraperitoneal injection (27-gauge 0.5-in. needle) 1 min and 15 min before the session, respectively. Both drugs were dissolved in 0.9% sodium chloride solution at concentrations appropriate for injection of each dose in a volume of 1 ml/kg. The placebo controls for the latter two drugs were 1 ml/kg of the vehicle.

The percentages of risky choice were calculated for each session by dividing the total number of choice trials completed on the lever that provided food pellets on a probabilistic basis by the total number of choice trials completed in that session. The rate of trial completion in each session was calculated by dividing the total number of trials completed

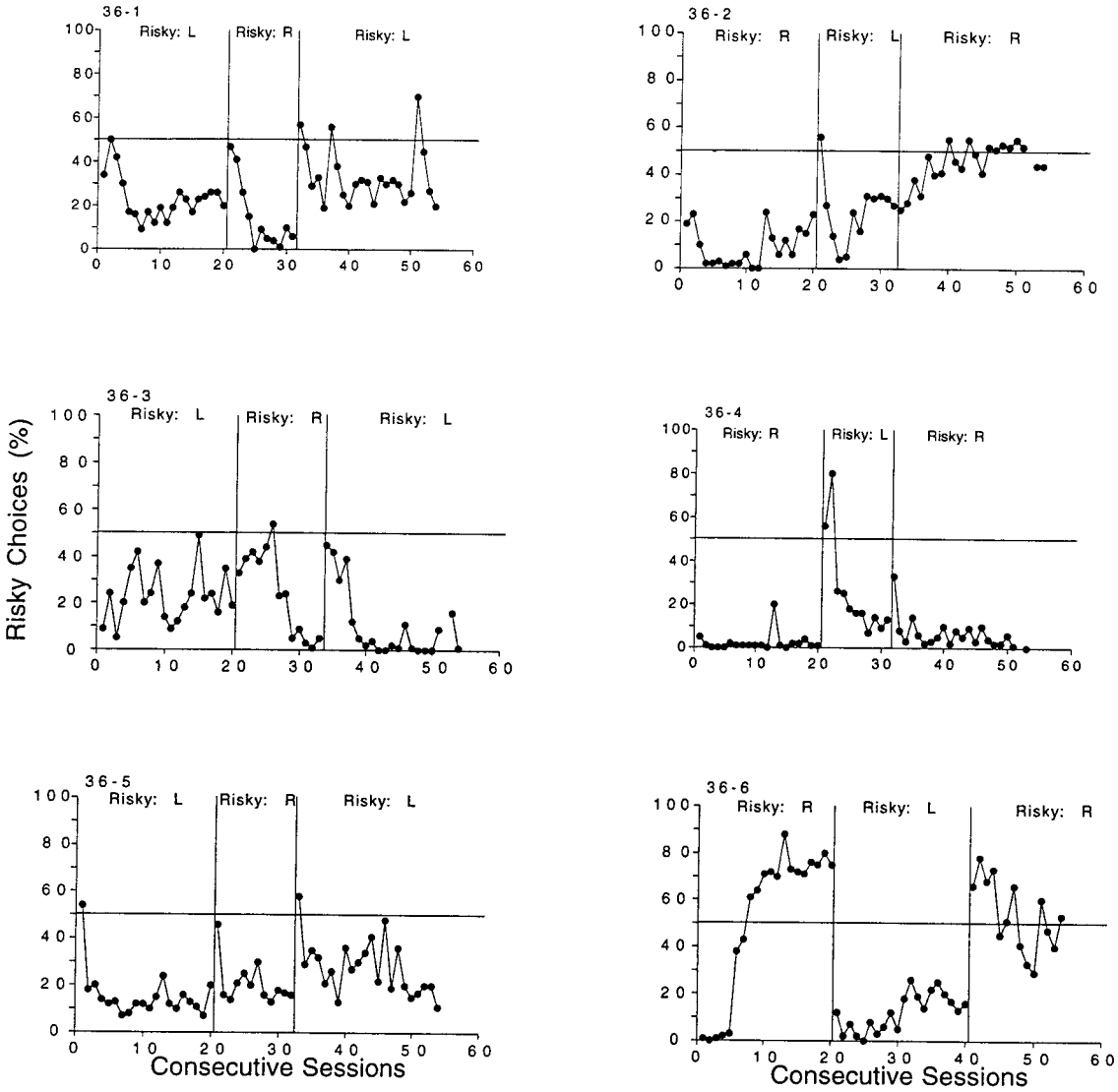


Fig. 1. Percentage of total lever choices that were for the lever on which responding produced 15 or 0 food pellets per reinforcement with a probability of .33 and .67, respectively, versus the lever on which an equal number of responses produced three pellets with a probability of 1.0. Responses on the former lever are characterized as the risky choice. For the 3 rats for which data are presented in the left set of panels, the risky choice initially was the left (L) lever; it was the right (R) lever for the 3 rats for which data are presented in the right set of panels. The contingencies were then reversed (middle section of each panel) and finally were returned to the original condition for each rat.

(including the 12 forced-choice trials) by the total session time minus the time spent in the ITI.

RESULTS

Lever-Reversal Condition

In the lever-reversal condition carried out after training under the FR 1 and ITI 20-s baseline condition, each rat's preference for the risky or the certain lever tracked the contingency when the contingencies were reversed between levers and again when they changed back to the original levers. As seen in Figure 1, 5 of the 6 rats responded predominantly on the certain lever across the 20 sessions before the contingencies were reversed (i.e., risky choice was less than 50% for

Rats 36-1 to 36-5 and usually was less than 30%). When the risky lever changed from being the left to the right lever for Rats 36-1, 36-3, and 36-5 and from the right to the left lever for Rats 36-2 and 36-4, the former 3 rats persisted in responding on the right lever and the latter 2 rats persisted in responding on the left lever, even though this resulted in fewer pellets, but this behavior occurred only in the first one or two sessions for most rats before risky choice decreased. The rat (36-6) that had a high probability of risky choice before the reversal of contingencies persisted in responding on the right lever after the reversal, which dramatically reduced baseline percentage of risky choice from about 80% to about 20%. When the contingencies were returned to the former lever assignments, all rats persisted in responding predominantly on the certain lever, which increased percentage of risky choice; but this time, perseverance on the risky lever continued for more sessions than previously for most rats, and risky choice remained higher than in the previous conditions for Rats 36-1, 36-2, and 36-6. Throughout the remainder of the experimental conditions, to be described below, the figures will show that percentages of risky choice under FR 1 ITI 20 s tended to remain in the same relative range as shown in the final condition of Figure 1 during the pharmacological manipulations under this set of parameters for all rats. By the behavioral manipulations though, as will be seen, the range shifted down for Rat 36-1 and up for Rat 36-5.

FR Manipulations

Figure 2 shows the percentage of choices of the risky lever when FR value was manipulated. In the last three sessions of the first FR 1 condition, all rats usually chose the risky alternative on fewer than 50% of the trials, and 4 of the 6 never chose the risky lever on more than 30% of the trials. Only Rat 36-5 chose the risky alternative approximately equally as often as the certain lever. As FR value increased, the relative frequency of choosing the risky lever decreased. At FR 8 and FR 16, the percentage of risky choice in the three sessions shown was usually zero but was below 10% for all 6 rats.

When the FR value returned to 1, percentage of choices of the risky lever increased for those 3 rats (36-2, 36-4, and 36-5) that initially had 20% or more risky choices at FR 1, but percentages were not as high as they had been in the previous FR 1 condition. When the FR 16 condition was replicated, none of the 6 rats made the risky choice.

Body weights across the last three sessions of each FR condition are given in Table 1. There was a slight tendency for weight to decrease at the higher FR values, as the percentage of risky choice decreased, for Rats 36-2, 36-4, 36-5, and 36-6, but the decreases were small. The largest percentage decrease was 3%.

Session duration, choice trials completed (if less than the total available), and rate of trial completion are provided in Table 2. During the first FR 1 condition and at FR 2, half the rats (36-1, 36-2, and 36-6) failed to complete all 93 available choice trials within the 90-min maximum session duration in one or two of the three sessions at each FR shown in Figure 2, but they completed 53 to 91 trials. Otherwise, sessions were completed in 45 to 82 min (medians were 52 to 54 min). As the FR requirement increased, session duration did not systematically increase for all rats; they usually completed all 93 choice trials within 60 to 80 min.

ITI Manipulations

Figure 3 shows the percentage of choices of the risky lever for the last three sessions at each ITI duration. When the ITI was the shortest (20 s), all rats preferred the certain lever. That is, they chose the risky alternative on less than 50% of the trials in most sessions, and 3 of the rats (36-1, 36-3, and 36-4) chose the risky alternative on less than 20% of the trials. At most, responses were distributed roughly equally between levers in some sessions.

As the ITI increased from 20 to 60 s, percentage of risky choice increased for 3 rats, decreased for 1 rat (36-5), and remained less than 20% for 2 rats (36-1 and 36-3). As the ITI increased from 60 to 120 s, however, percentage of risky choice increased for 5 of the 6 rats (albeit the percentage for Rat 36-3 never was above 10%); it remained between 80% and 100% for the 6th rat (36-6). When the ITI was 120 s, 5 of the 6 rats chose the risky alternative on more than 50% of the trials, and for 3 of the 5, risky choice was above 80%.

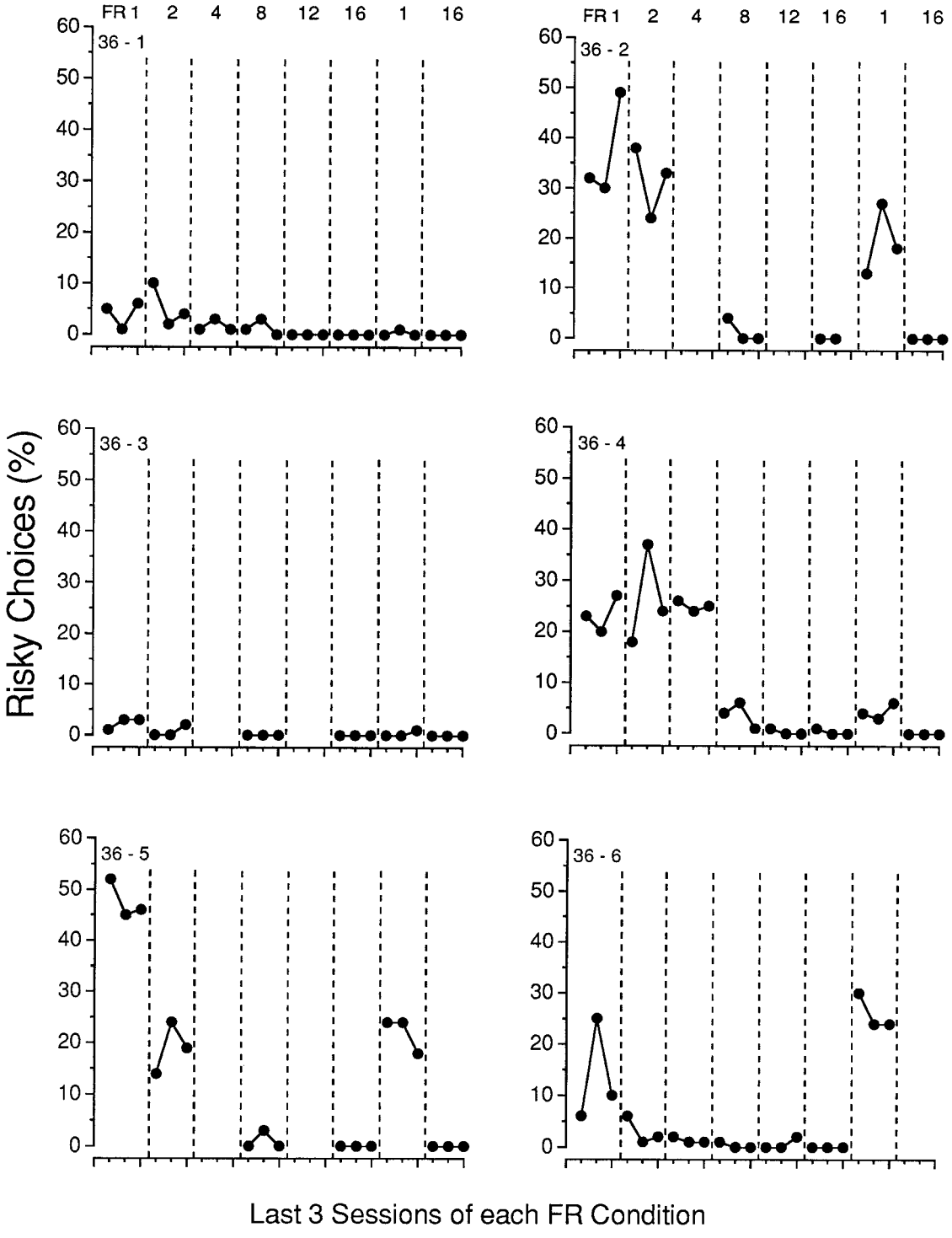


Fig. 2. Percentage of risky choices under a concurrent FR FR schedule of food delivery as a function of FR value. Each panel shows data for 1 of 6 rats across the last three sessions at the FR value at the top of each column. The *y* axis has been truncated at 60%. The FR values were studied in the order given across the top of the figure. Data are missing in some columns because not all rats were studied under each FR value.

Table 1

Mean body weight (in grams) in the last three sessions of sequential FR conditions.

	Rat					
FR	36-1	36-2	36-3	36-4	36-5	36-6
1	346	374	374	416	374	374
2	347	372	371	406	373	375
4	345			405		372
8	343	367	375	404	367	365
12	345			404		365
16	349	364	374	406	368	364
1	349	365	381	405	372	373
16	347	363	381	407	371	348

When the ITI was shortened to 20 s again, the percentage of risky choice decreased. All rats chose the risky alternative on fewer than 50% of trials. For 5 of the 6 rats, the percentages in the replication of the 20-s ITI condition were the same as or close to the percentages in the initial 20-s ITI condition. When the 80-s ITI condition was replicated, percentage of risky choice increased to a range that was either approximately the same as or higher than the range shown for the previous 80-s condition.

Number of choice trials completed, session duration (if less than 90 min), and rate of trial completion are provided in Table 3. In the first 20-s ITI condition, almost all rats completed the 93 free-choice trials that could be completed in each session. This was also true for most sessions at ITI 40 s. The number of choice trials completed per session necessarily decreased as the ITI increased further (although rats usually completed the maximum possible), and the number of pellets earned also decreased. Figure 4 shows the mean number of pellets earned during the last three sessions at each ITI. The rat that did not show greater than 10% risky choice

Table 2

Fixed-ratio (FR) value manipulations: Session durations (in minutes) and rate of trial completion (trials per minute excluding time in intertrial interval) for the last three sessions at each FR value for each rat for the sessions shown in Figure 2.

	Rat											
	36-1		36-2		36-3		36-4		36-5		36-6	
FR	Min	Rate	Min	Rate	Min	Rate	Min	Rate	Min	Rate	Min	Rate
1	90[a]	1.6	54	5.5	47	8.8	54	5.5	90[b]	1.7	<90	ND
	57	4.8	59	4.4	51	6.6	59	4.4	80	2.3	62	3.9
	90[c]	1.9	90[d]	1.0	51	6.6	51	6.6	90[e]	1.2	47	8.8
2	90[f]	1.6	90[g]	1.7	45	10.5	58	4.6	82	2.2	<90	ND
	46	9.5	52	6.2	46	9.5	55	5.2	90[g]	1.7	49	7.5
	90[h]	1.8	63	3.8	67	3.3	53	5.8	90[i]	1.8	52	6.2
4	53	5.8					54	5.5			55	5.2
	90[j]	1.3					53	5.8			54	5.5
	51	6.6					52	6.2			63	3.8
8	90[g]	1.7	55	5.2	73	2.8	53	5.8	65	3.5	83	2.2
	78	2.4	51	6.6	69	3.1	50	7.0	84	2.1	71	2.9
	54	5.5	48	8.1	57	4.8	48	8.1	65	3.5	72	2.8
12	70	3.0					51	6.6			90[h]	1.8
	62	3.9					52	6.2			90[k]	1.9
	76	2.6					52	6.2			89	1.9
16	79	2.4	56	5.0	72	2.8	55	5.2	78	2.4	88	2.0
	70	3.0	61	4.0	72	2.8	54	5.5	73	2.8	85	2.1
	67	3.3	54	5.5	70	3.0	56	5.0	64	3.6	90[l]	1.5
1	56	5.0	68	3.2	51	6.6	55	5.2	79	2.4	82	2.2
	50	7.0	63	3.8	43	13.1	44	11.7	63	3.8	61	4.0
	52	6.2	77	2.5	44	11.7	47	8.8	53	5.8	53	5.8
16	67	3.3	53	5.8	61	4.0	52	6.2	64	3.6	80	2.3
	63	3.8	54	5.5	65	3.5	54	5.5	64	3.6	85	2.1
	64	3.6	53	5.8	68	3.2	56	5.0	71	2.9	90[m]	1.6

Note. ND = no data (session-duration data lost, so rate could not be calculated). The number of free-choice trials was 93 unless otherwise indicated by a footnote, as follows: [a] 80, [b] 87, [c] 91, [d] 53, [e] 64, [f] 82, [g] 85, [h] 89, [i] 88, [j] 70, [k] 92, [l] 78, [m] 83.

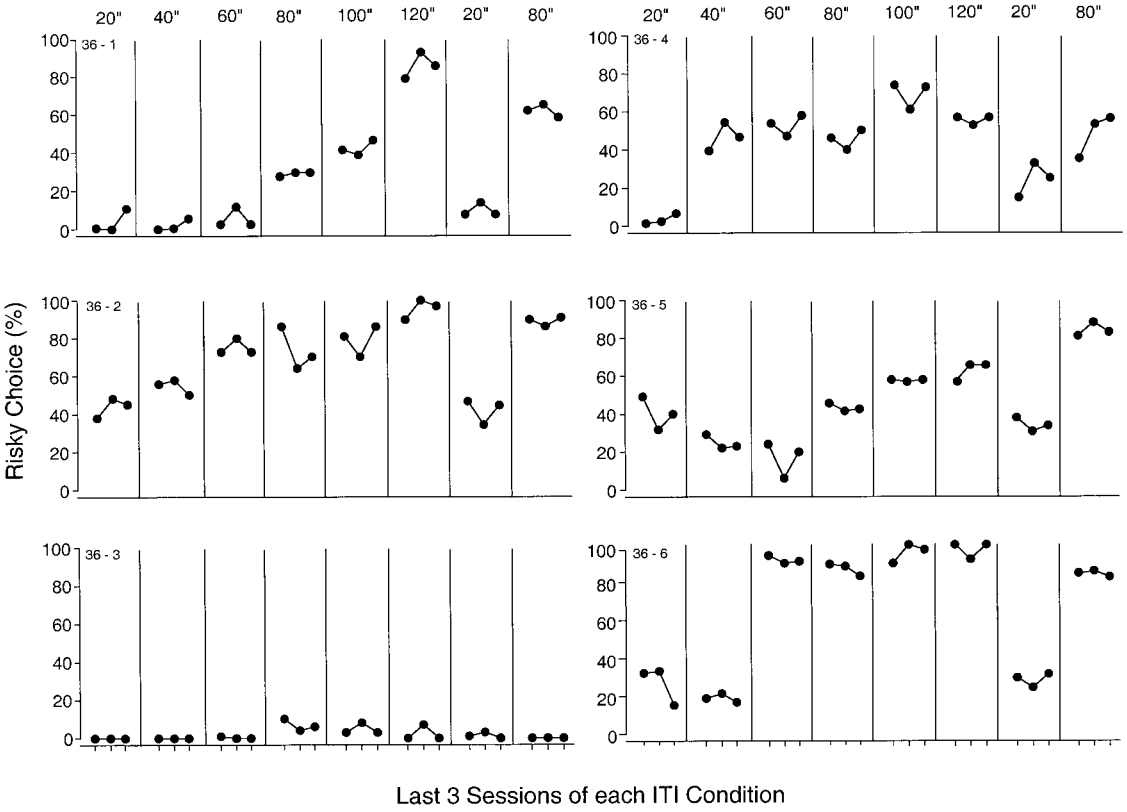


Fig. 3. Percentage of risky choices under a concurrent FR 1 FR 1 schedule of food delivery as a function of ITI duration. Each panel shows data for 1 of 6 rats across the last three sessions at the ITI value shown at the top of each column. The ITI values were studied in the order shown across the top of the figure.

(Rat 36-3) experienced the greatest decrease in mean number of pellets earned per session at ITI values of 80 to 120 s.

Figure 5 shows mean body weights during the last three sessions at each ITI value. As ITI increased, body weight decreased for all rats. Decreases in body weight first appeared at ITI 60 s for Rats 36-1, 36-3, and 36-5 and at ITI 80 s for Rats 36-2, 36-4, and 36-6. They increased upon return to the 20-s ITI for all 6 rats and then decreased again, if only slightly, for 5 of the 6 rats during replication of the 80-s ITI condition. The ITI at which bodyweight changes first occurred for each rat did not correspond with the ITI at which increases in risky choice first occurred, and the order of these changes was not the same across rats. For Rat 36-1, for example, body weight decreased in the 60-s ITI and risky choice increased in the 80-s ITI; but for Rat 36-2, risky choice increased in the 40-s ITI condition but body weight did not decrease until the 80-s ITI condition.

Ethanol

Figure 6 shows that during the 20-s ITI condition, baseline percentage of risky choice was less than 20% for 2 rats (36-3 and 36-4) and was between 15% and 65% for the other 4 rats. Ethanol decreased risky choice below the baseline range and below the vehicle control in the 4 rats for which it was possible to detect decreases in this measure. The highest ethanol dose (3 g/kg) decreased risky choice to zero or virtually zero in all 4 of them; for 2 rats (36-1 and 36-5), risky choice decreased also at lower ethanol doses. Only Rat 36-6 showed an increase, albeit slight, after ethanol administration.

Use of the 80-s ITI resulted in a higher baseline range of percentages of risky choice than the 20-s ITI for 4 rats (36-2, 36-4, 36-5,

Table 3

Intertrial-interval (ITI) manipulations: Total number of free-choice trials and overall rate of trial completion (total free- and forced-choice trials per minute excluding time in ITI) for the last three sessions at each ITI for each rat for the sessions shown in Figure 3.

	Rat											
	36-1		36-2		36-3		36-4		36-5		36-6	
ITI (s)	No.	Rate	No.	Rate	No.	Rate	No.	Rate	No.	Rate	No.	Rate
20	93[a]	5.2	93[b]	4.6	93[c]	10.5	93[d]	17.5	78	1.5	90	1.8
	93[e]	7.0	84	1.7	93[f]	13.1	93[g]	15.0	93[h]	2.3	93[i]	4.2
	93[j]	2.1	93[k]	6.2	93[c]	10.5	93[c]	10.5	93[l]	2.0	93[i]	4.2
40	93[m]	9.5	93[m]	9.5	93[n]	15.0	93[o]	7.5	92	5.0	86	4.0
	93[p]	13.1	93[q]	5.5	93[n]	15.0	93[r]	5.8	93[q]	5.5	91	4.8
	87	4.1	67	2.1	93[n]	15.0	89	4.5	93[o]	7.5	93[l]	6.2
60	70	10.2	64	5.4	71	11.9	68	8.0	67	7.2	58	3.5
	69	9.0	69	9.0	72	14.0	71	11.9	71	11.9	61	4.3
	70	10.2	67	7.2	71	11.9	67	7.2	71	11.9	56	3.1
80	50	8.5	50	8.5	51	10.5	50	8.5	49	7.0	45	4.1
	50	8.5	50	8.5	50	8.5	50	8.5	51	10.5	41	2.7
	47	5.2	50	8.5	51	10.5	50	8.5	38	2.1	41	2.7
120	27	3.2	30	7.0	30	7.0	30	7.0	30	7.0	26	2.7
	29	5.1	29	5.1	30	7.0	30	7.0	29	5.1	25	2.3
	29	5.1	29	5.1	30	7.0	30	7.0	30	7.0	25	2.3
20	92	1.9	93[s]	3.3	93[k]	6.2	93[t]	3.4	77	1.5	93[u]	3.9
	93[v]	3.8	93[n]	2.5	93[s]	3.3	93[w]	5.0	90	1.8	93[x]	4.8
	84	1.7	77	1.5	93[k]	6.2	93[y]	5.5	93[z]	2.2	93[aa]	3.1
80	48	6.0	50	8.5	51	10.5	50	8.5	42	3.0	40	2.5
	47	5.2	50	8.5	51	10.5	50	8.5	42	3.0	43	3.3
	46	4.6	45	4.1	51	10.5	49	7.0	48	6.0	40	2.5

Note. Session duration was 90 min unless otherwise indicated by a footnote, as follows: [a] 55, [b] 58, [c] 45, [d] 41, [e] 50, [f] 43, [g] 42, [h] 80, [i] 60, [j] 86, [k] 52, [l] 87, [m] 81, [n] 77, [o] 84, [p] 78, [q] 89, [r] 88, [s] 67, [t] 66, [u] 62, [v] 63, [w] 56, [x] 57, [y] 54, [z] 83, [aa] 69.

and 36-6). Ethanol decreased risky choice below baseline and below the vehicle controls for 3 rats (i.e., 36-2, 36-4, and 36-5). Rat 36-6 had the highest baseline percentage of risky choice at the 80-s ITI, but did not show any decrease after ethanol administration, which was in contrast to the results for this rat at the 20-s ITI. This rat did again show an increase in risky choice at the lower doses of ethanol, however.

For the other 2 rats (36-1 and 36-3), the baseline range was not above zero, so decreases in risky choice could not be observed. This baseline range at the 80-s ITI was decreased for Rat 36-1 compared to the 20-s ITI condition. For Rat 36-3, the upper end of the range was even lower than under the 20-s ITI. These 2 rats showed increases in risky choice after vehicle administration, and Rat 36-1 showed an increase at 1 g/kg ethanol.

Repeating one or more doses in the 80-s ITI condition (Figure 6) confirmed two of the four effects of vehicle (for Rats 36-1 and 36-2), one of three rate increases after ethanol (for Rat 36-6), and one of two rate decreases (for Rat 36-5).

Tables 4 and 5 present total number of trials completed, session duration, and rate of trial completion for the test sessions shown in Figure 6 for the 20- and 80-s ITI conditions, respectively. Rate of trial completion was decreased for all 6 rats by 2.5 or 3.0 g/kg ethanol and by lower doses in 4 rats, but only 1 rat failed to complete any trials at a dose and most rats always completed 60 to 105 trials. In the 80-s ITI condition, the rats completed fewer trials after vehicle compared to the 20-s ITI condition (i.e., 38 to 62 trials in 90 min compared to 72 to 105 in 44 to 90 min at the 20-s ITI). In contrast to the 20-s ITI condition, rate of trial completion remained within the range for vehicle in all except two tests in which a rat failed to complete even the forced-choice trials (at 2.0 or 3.0 g/kg for 2 rats).

Phencyclidine

Figure 7 shows that during the 20-s ITI condition, phencyclidine produced an effect dif-

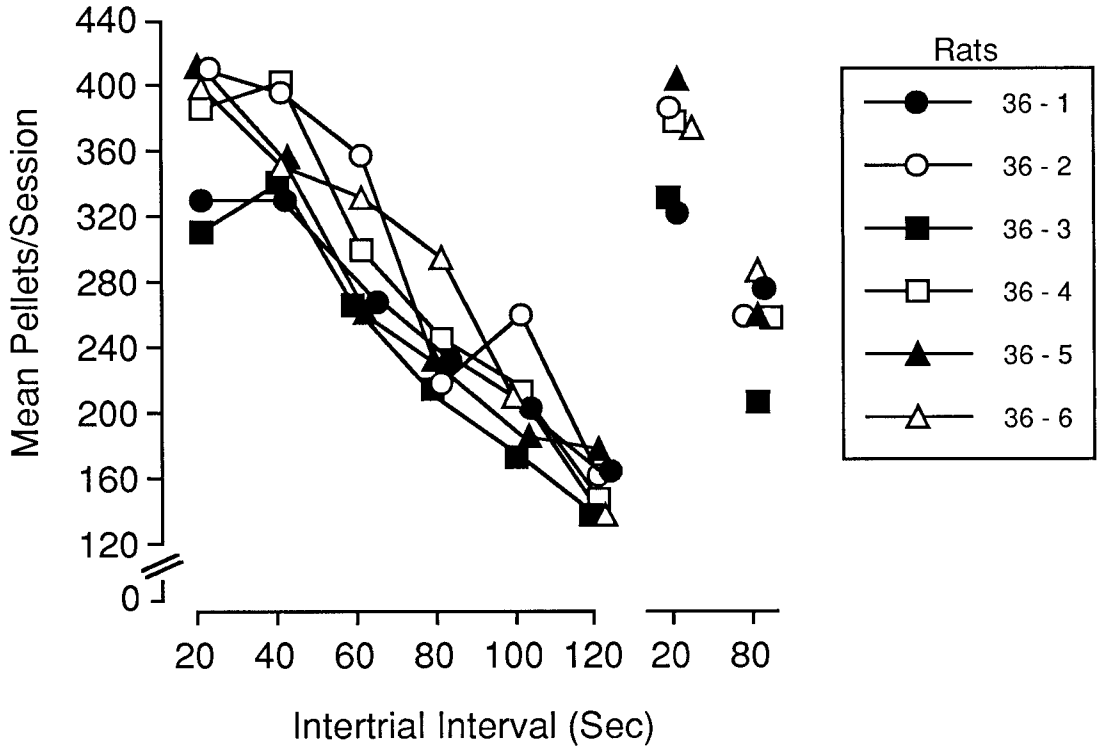


Fig. 4. Mean number of pellets obtained per session as a function of ITI under a concurrent FR 1 FR 1 schedule of food delivery for each of 6 rats. Each mean is for the last three sessions at each ITI. The ITI values were studied in the order shown on the *x* axis; the unconnected points over the 20-s and 80-s ITI conditions are for replications after the ascending series of ITI values was completed. Note that the *y* axis is truncated below 120 pellets per session.

ferent from baseline and from the effect of injection of vehicle in only 1 rat (36-2); that is, risky choice decreased slightly outside of baseline at two doses.

During the 80-s ITI condition shown in Figure 7, phencyclidine decreased the percentage of risky choice below the baseline range and below vehicle in all rats for which it was possible to detect a decrease in this measure, and it increased the percentage of risky choice in Rat 36-3. The dose–effect curve was repeated in all 5 rats studied, and significant effects of PCP were found again for 4 of them.

Table 4 shows that one or more doses of PCP increased rate of trial completion above that after vehicle in 4 of the 5 rats studied. Higher doses decreased rate of trial completion in 3 of those rats and all PCP doses decreased rate of trial completion for 1 other rat, yet number of trials completed ranged from 87 to 105 for all rats after PCP even when rate of trial completion decreased. Table 5 shows that in the 80-s ITI condition, the rate of trial completion (trials per minute) was increased compared to vehicle in only 1 rat, decreased in 2 rats, and both increased and decreased in 2 rats. Yet number of trials completed ranged from 49 to 62 even when rates were decreased.

d-*Amphetamine*

Figure 8 shows that at the 20-s ITI *d*-amphetamine increased risky choice above baseline in a dose-related manner in 2 rats (36-4 and 36-5) that had low baseline ranges of percentage of risky choice. It arguably increased risky choice in a dose-related manner for Rat 36-3 also (the first vehicle injection increased risky choice slightly). Rat 36-6 showed an increase in risky choice at the lowest dose (0.32 mg/kg), but this increase was not replicated, and the first vehicle injection produced a greater increase than the one at 0.32 mg/kg. Rat 36-1 showed no change in risky choice. Rat 36-2, the rat with the highest baseline

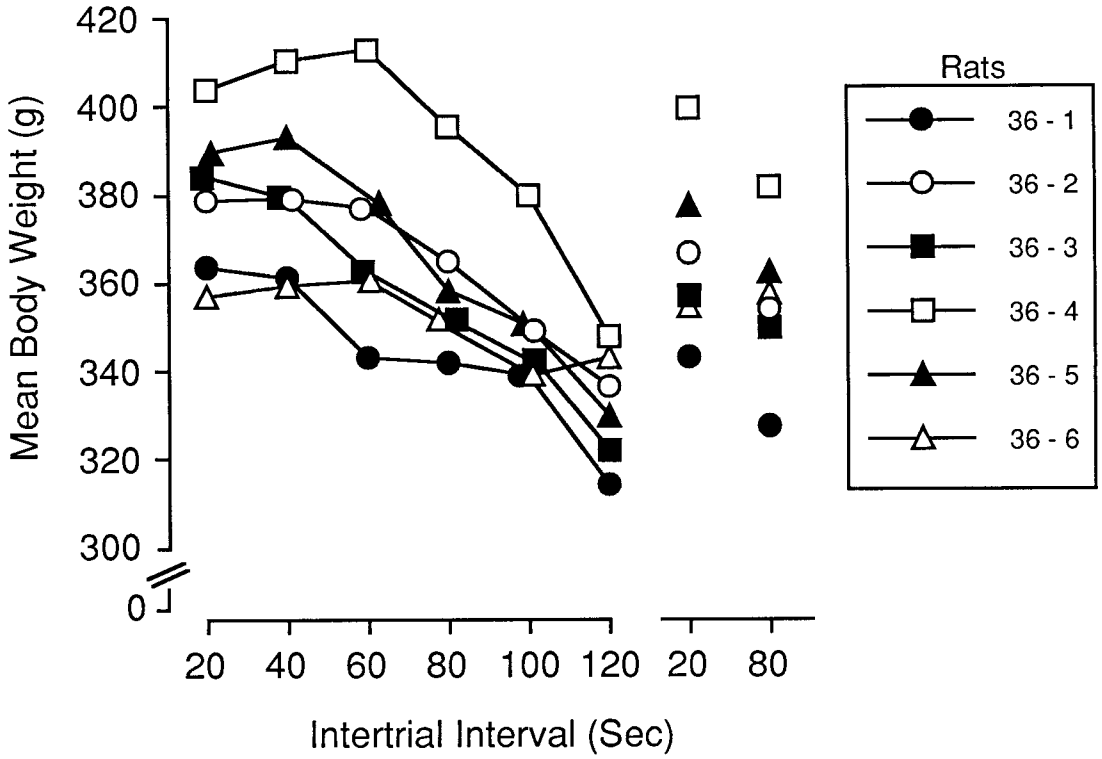


Fig. 5. Mean body weight as a function of ITI for each of 6 rats. The ITI values were studied in the order shown on the *x* axis; the unconnected points over the 20-s and 80-s ITI conditions are for replications after the ascending series of ITI values was completed. The total number of sessions at each ITI value ranged from 3 to 18 across rats. Each mean is for the last three sessions at each ITI. Note that the *y* axis is truncated below 300 g.

range, arguably showed a decrease in risky choice (the second vehicle injection decreased risky choice slightly).

During the 80-s ITI condition, the baseline range of risky choice was higher in 4 of the 6 rats relative to the 20-s ITI condition. For those rats (36-2, 36-4, 36-5, and 36-6), *d*-amphetamine decreased percentages of risky choice in a dose-related manner. The baseline range of risky choice was lower than in the 20-s ITI condition for Rats 36-1 and 36-3, and dose-related increases in percentage of risky choice occurred. Repeating the dose–effect determinations replicated the basic finding of decreases in high percentages of risky choice and increases in low percentages of risky choice in all 6 rats.

Table 4 shows that rate of trial completion was an inverted U-shaped function of *d*-amphetamine dose for 5 of the 6 rats in the 20-s ITI condition. The lowest dose of *d*-amphetamine (0.32 mg/kg) at least doubled the rate of trials for those 5 rats, and 1.0 mg/kg also increased trial rate in 4 of the same rats. After 3.2 mg/kg, rates were decreased in 3 rats; 2 of those failed to complete even one forced-choice trial. Complete response suppression occurred after 5.6 mg/kg in all rats tested.

Table 5 shows that in the 80-s ITI condition, rate of trial completion increased at one or more doses for all rats except the rat with the highest rate of trial completion (10.5 trials per minute for Rat 36-3) after vehicle. Rate of trial completion decreased for all but 1 rat in tests with 3.2 mg/kg such that no choice trials were completed by 5 rats in at least one test at this dose.

DISCUSSION

Under the baseline conditions of FR 1 and ITI 20 s, when the rats usually completed all the available trials in less than the 90-min maximum session length, most rats showed risk aversion by responding on the certain le-

ver in 70% or more of the trials in each session. A minority of the rats responded on the two levers about equally. Although 100% risky lever choice would have maximized the number of pellets that could be obtained to over 1,000 per session under baseline conditions, the rats still obtained about 350 pellets (almost 16 g) per session. This amount of food maintained weights at 350 to 400 g, which is relatively high as a running weight when food is the reinforcer in this strain of rats (Ator, 1991).

The results of the baseline condition were consistent with predictions of risk-sensitive foraging theories (Kacelnik & Bateson, 1996). That is, an organism should be risk averse when the food supply is sufficient to meet caloric requirements (a positive energy budget) and risk prone when it is not (a negative energy budget). The present study showed that this outcome also occurred under a condition in which the period of food access was relatively short (i.e., 6% of a 24-hr period). In another study with rats in which the period of food access was longer (3 hr or 12% of a 24-hr period), Ito, Takatsuru, and Saeki (2000) reported approximately 60% to 70% choice of the constant alternative under a positive energy budget and a slight (approximately 50% to 60% choice) shift to the risky alternative under a negative energy budget. In the one laboratory study conducted under similar restricted-access feeding conditions with birds, however, gray jays were risk prone under both positive and negative energy budgets (Ha et al., 1990). One of a number of procedural variables that may have been important was that the birds chose between two variable options rather than between a constant and variable option.

The results of the baseline condition also are consistent with previous findings on the variables that determine preference for a variable option when energy budget is positive. When choices have been presented between options that have variable versus fixed searching time, delay to reward, or number of responses required, animals have preferred the higher variance option. When variance has been in the amount of food delivered per reinforcer, however, preference has been for the lower variance option (Kacelnik & Bateson, 1996).

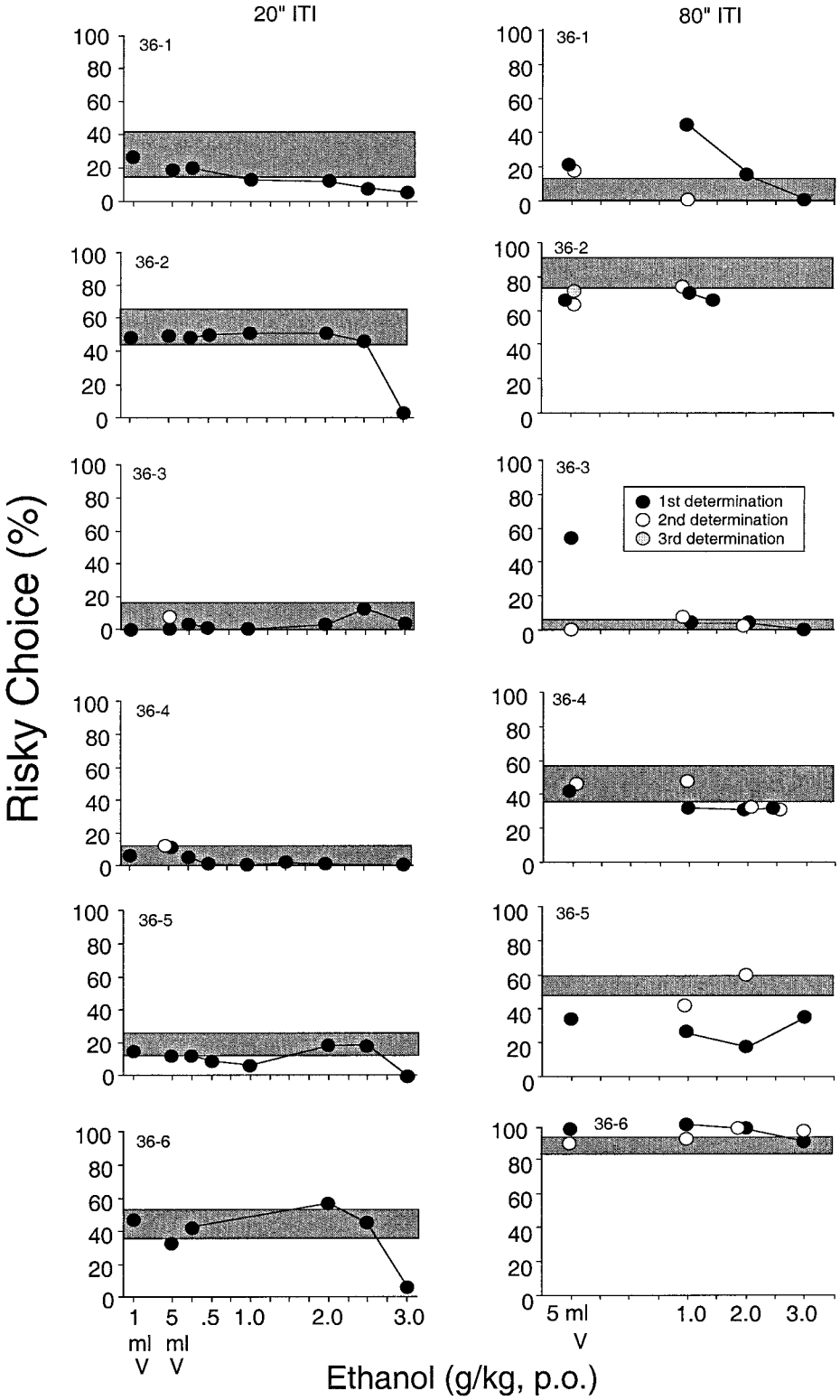
Behavioral Manipulations

Fixed ratio. When the response requirement for food delivery was increased, the rats showed even greater risk aversion, if possible, than under the baseline condition. Under the highest requirement (FR 16), they typically did not respond at all on the risky lever. Although a consequence of the higher response requirement combined with the persistence of risk aversion was to reduce slightly the total number of pellets received for some rats in some sessions, body weights did not decrease. Thus although increasing the effort to produce food delivery might have been expected to decrease risk aversion in the absence of a negative energy budget, it did not function in the same way as markedly decreasing opportunities to obtain food.

In studies by Ha (1991; Ha et al., 1990), wild-caught gray jays chose between response opportunities that had lower and higher variances in the probability of food reinforcement under equal-valued concurrent variable-ratio (VR) VR schedules; VR value was manipulated from 10 to 80. Unlike the risk aversion shown by the rats in the present study, most of the gray jays were risk prone (i.e., responded predominantly on the high variance option) or showed no preference under all conditions. Because number of responses required apparently has not been manipulated in other studies related to risky choice, the variables responsible for risk aversion in the present study and risk proneness in the Ha studies remain to be determined.

The present results also differ from what might be predicted by extension of the unit price analysis, in behavioral economic terms, of each choice. Unit price of each pellet delivered under each option can be defined as FR value divided by the product of the number of pellets and the probability they will be delivered (Hursh, Raslear, Shurtleff, Bauman, & Simmons, 1988). Using this calculation, the certain lever required a higher unit price per pellet than the risky lever across all FR conditions.

Intertrial interval. When ITI was increased, the number of trials that could be completed within the 90-min maximum session duration decreased. Although total pellets available had to decrease as ITI increased, regardless of lever choice, responding on the risky lever


20" ITI
80" ITI
36-1
36-2
36-3
36-4
36-5
36-6
Risky Choice (%)
1st determination
2nd determination
3rd determination
1 ml V
5 ml V
.5
1.0
2.0
3.0
Ethanol (g/kg, p.o.)

on 100% of the trials would have maximized pellets obtained (e.g., at the 60-s ITI, total pellets available would have stayed above 300, about 14 g). In fact, the percentage of trials completed on the risky lever did increase above 50% by the 60-s ITI for half the rats. By the 120-s ITI condition, risky choice was between 60% and 100% in at least one ITI condition for 5 of the 6 rats.

Inspection of the data for individual rats indicated that as ITI increased, mean number of pellets per session decreased under either the 40-s or 60-s ITI, and weight decreased under either the same or the next higher ITI condition. Thus, the obtained increases in risky choice as ITI increased were consistent with predictions of risk-sensitive foraging theory. For half the rats, an increase in risky choice above the percentages in the 20-s ITI condition first occurred in the ITI condition that followed a decrease in pellets or followed decreases in both pellets and weight, but for the other half of the rats, an increase in risky choice occurred in the ITI condition that preceded the decrease in pellets. Also, during the replication of the 80-s ITI condition, risky choice again decreased despite the fact that body weights had not substantially decreased. There was no relation between mean pellets per session or body weight and whether increase in risky choice preceded or followed the decrease in pellets or weight. These data suggest that it is possible that experiencing the longer ITI per se may have been sufficient to increase choice of the risky lever.

As ITI increased in the present experiment, total pellets available decreased, which represented a shift from a positive to a negative energy budget, and there was an increase in responding on the risky lever. Studies of risky choice in animals other than rats also found that when ITI was manipulated, sparrows, juncos, and common shrews were risk averse on positive energy budgets and risk prone on negative energy budgets (Barnard & Brown, 1985; Caraco, 1981, 1983; Caraco, Martindale, & Whittam, 1980). All of these results are consistent with risk-sensitive foraging theories that predict a direct relationship between risk aversion and energy budget.

In the operant behavior literature, probabilistic reinforcers have been seen as functionally similar to delayed reinforcers. That is, Rachlin, Logue, Gibbon, and Frankel (1986) proposed that when a reinforcer is delivered with a probability of less than 1.0, the effect on behavior is the same as if the reinforcer were delayed. In an equation developed to equate delay and probability of reinforcement, the expected delay to a reinforcer is a function of trial duration (including the ITI), divided by probability of reinforcer delivery, minus the duration of the ITI. This equation thus predicts that increasing the delay to a probabilistic reinforcer by increasing the length of the ITI in the present experiment should have resulted in greater risk aversion. In fact, previous studies, which used procedures considerably different from the present one, have reported that increases in ITI either had no systematic effect on choice (e.g., Lawes & Perrin, 1995; Lea, 1979; Mazur, 1989; Spetch, Mondloch, Belke, & Dunn, 1994) or decreased risky choice (Mazur & Romano, 1992; Rachlin et al., 1986; Silberberg et al., 1988).

Another account of the relationship between delay and probability that can be applied to the present results, however, is provided by delay-reduction theory (DRT; Squires & Fantino, 1971). Developed to account for choice in concurrent variable-interval schedules, DRT has been applied to a wide range of investigations involving choice, including self-control (Ito & Asaki, 1982; Navarick & Fantino, 1976), foraging (Abarca & Fantino, 1982; Fantino & Abarca, 1985), and probabilistic reinforcement (Abarca, Fantino, & Ito, 1985; see also Fantino, Preston, &

←

Fig. 6. Percentage of risky choices under a concurrent FR 1 FR 1 schedule of food delivery as a function of dose of ethanol or its vehicle (V) delivered to the stomach (per os, p.o.) when the ITI was 20 s (left column) and when it was 80 s (right column). The shaded area in each panel encompasses the range of percentages of risky choice during the last five sessions prior to beginning drug testing in each ITI condition. Each point represents a single session, and the lines connect the first occasion on which the effects of the dose were determined. When no choice trials were completed, no point was plotted; but whether any forced trials were completed, and other data, can be seen in Tables 4 and 5 for the 20-s and 80-s ITI conditions, respectively.

Table 4

20-s intertrial interval: Effects of ethanol, phencyclidine, *d*-amphetamine, and their vehicles (V) on total number of completed trials (i.e., forced choice plus free choice), session duration (in minutes), and overall rate of trial completion (trials per minute, excluding time spent in timeouts) for sessions shown in Figures 6, 7, and 8.

	Rat																	
	36-1			36-2			36-3			36-4			36-5			36-6		
Dose	No.	Min	Rate	No.	Min	Rate	No.	Min	Rate	No.	Min	Rate	No.	Min	Rate	No.	Min	Rate
Ethanol (g/kg)																		
V(ml)	91	90	1.5	96	90	1.7	105	44	11.7	105	51	6.6	105	67	3.3	105	58	4.6
1	98	90	1.7	80	90	1.3	102	90	1.8	105	45	10.5	72	90	1.1	105	68	3.2
5							105	50	7.0	105	48	8.1						
0.25	91	90	1.5	91	90	1.5	105	50	7.0	105	52	6.2	86	90	1.4	105	73	2.8
0.5				105	57	4.8	105	59	4.4	105	58	4.6	105	81	2.3			
1.0	84	90	1.4	94	90	1.6	105	67	3.3	105	52	6.2	96	90	1.7			
1.5										105	50	7.0						
2.0	85	90	1.4	95	90	1.6	105	74	2.7	105	58	4.6	63	90	0.9	82	90	1.3
2.5	99	90	1.7	68	90	1.0	75	90	1.2	0	90	0.0	105	85	2.1	105	74	2.7
3.0	74	90	1.1	90	90	1.5	87	90	1.4	105	84	2.1	27	90	0.3	65	90	1.0
Phencyclidine (mg/kg)																		
V	93	90	1.6	97	90	1.7	105	62	3.9	105	52	6.2				105	80	2.3
	81	90	1.3	97	90	1.7	105	70	3.0	105	52	6.2				76	90	1.2
																105	84	2.1
0.32	83	90	1.3	105	60	4.2	105	49	7.5	105	57	4.8						
1.0	105	66	3.4	87	90	1.4	105	89	1.9	105	53	5.8				105	52	6.2
3.2				105	69	3.1	88	90	1.4	105	86	2.1				105	69	3.1
d-amphetamine (mg/kg)																		
V	77	90	1.2	102	90	1.8	96	90	1.7	105	67	3.3	84	90	1.4	63	90	0.9
				105	54	5.5	105	90	1.9							86	90	1.4
0.32	105	76	2.6	105	75	2.6	105	57	4.8	105	50	7.0	105	69	3.1	101	90	1.8
																102	90	1.8
1.0	96	90	1.7	100	90	1.8	105	60	4.2	82	90	1.3	105	66	3.4	105	68	3.2
1.8	105	86	2.1	95	90	1.6	101	90	1.8	82	90	1.3	105	77	2.5	60	90	0.9
3.2	81	90	1.3	103	90	1.8	38	90	0.5	105	57	4.8	0	90	0.0	0	90	0.0
5.6	0	90	0.0	0	90	0.0	0	90	0.0	0	90	0.0						

Dunn, 1993). With respect to food reinforcers, the DRT model proposes that the value of a food-associated stimulus depends not only on the delay to food delivery in the presence of that stimulus but also on the overall average time to food delivery. In the present study, the delay to reinforcement when the certain lever was chosen was short (food was delivered on 100% of trials) but was longer when the risky lever was chosen (because pellets were not presented on two thirds of the trials). Thus the difference between these two ''delays'' was large when the ITI was short (e.g., 20 s) and smaller when the ITI was long (e.g., 120 s). For choices that differ in reinforcer magnitude, as in the present study, the effects of reinforcer magnitude should be more evident at the longer delays, and preference could be predicted to switch from the certain to the risky alternative, as was seen in the present results. Self-control choice studies also have shown that immediate reinforcers are preferred to delayed reinforcers, except that if the delay to the more immediate but smaller reinforcer and to the longer delayed but larger reinforcer are increased simultaneously, preference shifts from the shorter delayed to the longer delayed reinforcer (Ainslie, 1974; Logue, Rodriguez, Peña-Correal, & Mauro, 1984).

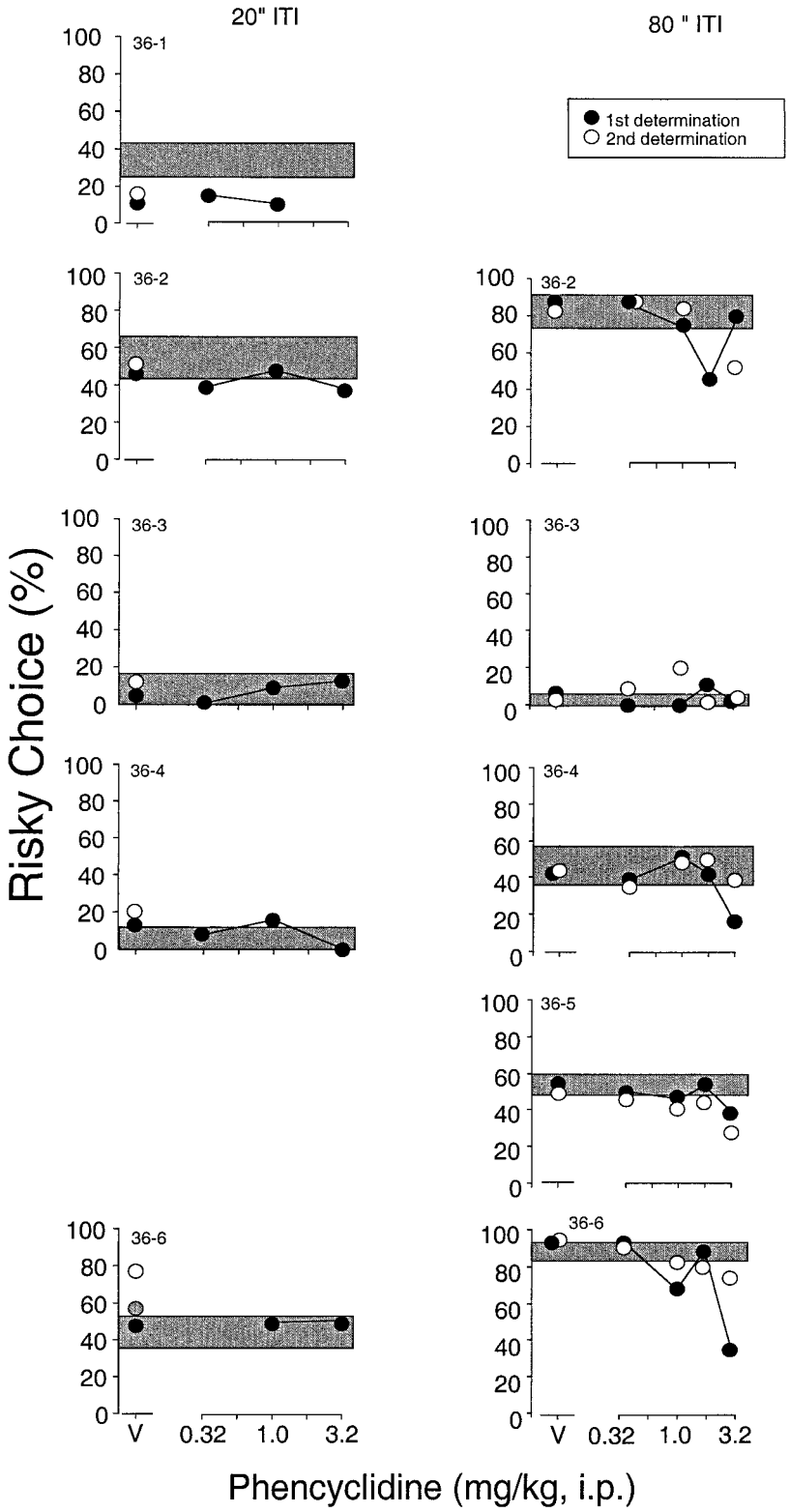
Previous studies of risky choice in rats have not manipulated ITI, but they have investigated the effects of decreasing the number of trials per session, which was concomitant to increasing the ITI in the present study. Kagel, MacDonald, Battalio, White, and Green (1986) found that rats were risk averse on positive and balanced energy budgets and

Table 5

80-s intertrial interval: Effects of ethanol, phencyclidine, *d*-amphetamine, and their vehicles (V) on total number of completed trials (i.e., forced choice plus free choice), session duration (in minutes), and overall rate of trial completion (trials per minute, excluding time spent in timeouts) for sessions shown in Figures 6, 7, and 8.

	Rat																	
	36-1			36-2			36-3			36-4			36-5			36-6		
Dose	No.	Min	Rate	No.	Min	Rate	No.	Min	Rate	No.	Min	Rate	No.	Min	Rate	No.	Min	Rate
Ethanol (g/kg)																		
5-ml V	58	90	4.6	62	90	8.4	38	90	1.0	62	90	8.4	56	90	3.7	56	90	3.6
	46	90	1.6	61	90	7.0	62	90	8.4	60	90	6.0				58	90	4.6
				55	90	3.3												
1.0	58	90	4.6	58	90	4.6	62	90	8.4	62	90	8.4	61	90	7.0	55	90	3.3
	59	90	5.2	59	90	5.2	62	90	8.4	60	90	6.0	56	90	3.6	51	90	2.3
1.5				58	90	4.6												
2.0	59	90	5.2	0	90	0.0	59	90	5.2	61	90	7.0	61	90	7.0	54	90	3.0
							62	90	8.4	60	90	6.0	59	90	5.2	49	90	2.0
2.5										58	90	4.6						
										56	90	3.6						
3.0	56	90	3.6				61	90	7.0	4	90	0.05	57	90	4.1	53	90	2.7
																53	90	2.7
Phencyclidine (mg/kg)																		
V				61	90	7.0	63	90	10.5	62	90	8.4	61	90	7.0	55	90	3.3
				60	90	6.0	63	90	10.5	62	90	8.4	49	90	2.0	54	90	3.0
0.32				57	90	4.1	63	90	10.5	63	90	10.5	62	90	8.4	54	90	3.0
				60	90	6.0	62	90	8.4	63	90	10.5	60	90	6.0	55	90	3.3
1.0				59	90	5.2	63	90	10.5	61	90	7.0	62	90	8.4	50	90	2.1
				61	90	7.0	63	90	10.5	62	90	8.4	60	90	6.0	54	90	3.0
1.8				53	90	2.7	59	90	5.2	62	90	8.4	62	90	8.4	57	90	4.1
							63	90	10.5	62	90	8.4	59	90	5.2	59	90	5.2
3.2				60	90	6.0	58	90	4.6	54	90	3.0	59	90	5.2	49	90	2.0
				58	90	4.6	49	90	2.0	60	90	6.0	61	90	7.0	58	90	4.6
d-amphetamine (mg/kg)																		
V	61	90	7.0	58	90	4.6	63	90	10.5	62	90	8.4	57	90	4.1	51	90	2.3
	61	90	7.0	59	90	5.2	63	90	10.5	62	90	8.4	61	90	7.0	57	90	4.1
													62	90	8.4			
0.32	61	90	7.0	60	90	6.0	54	90	3.0	62	90	8.4	62	90	8.4	55	90	3.3
	60	90	6.0	60	90	6.0	63	90	10.5	63	90	10.5	62	90	8.4	58	90	4.6
1.0	61	90	7.0	62	90	8.4	62	90	8.4	62	90	8.4	63	90	10.5	60	90	6.0
	60	90	6.0	61	90	7.0	62	90	8.4	63	90	10.5	63	90	10.5	61	90	7.0
1.8	61	90	7.0	60	90	6.0	34	90	0.8	43	90	1.3	63	90	10.5	60	90	6.0
	62	90	8.4	36	90	0.9	44	90	1.4	62	90	8.4	25	90	0.4	19	90	0.3
3.2	22	90	0.4	4	90	0.05	17	90	0.3	0	90	0.0	11	90	0.2	60	90	6.0
	6	90	0.1				52	90	2.5	21	90	0.3				0	90	0.0
5.6							1	90	0.01									
							0	90	0.0									

showed no preference on negative energy budgets. Hastjarjo et al. (1990) found decreases in percentages of risky choice when number of trials per session decreased, despite decreases in the number of pellets earned and in body weight. They speculated that this risk aversion when trials decreased was a result of increased day-to-day variance in reinforcers as the number of trials decreased. Although the results of Kagel et al. and Hastjarjo et al. differ from each other, both sets of results differ from the present finding, in which a clear increase in risky choice occurred as ITI increased and trials per session decreased. The critical difference in results may be due to the changes in delay to reinforcement that occur as ITI changes, which do not occur when the number of trials per session is simply manipulated. Although day-to-day reinforcer variability may indeed


20" ITI
80 " ITI
1st determination
2nd determination
36-1
36-2
36-3
36-4
36-5
36-6
Risky Choice (%)
100
80
60
40
20
0
V
0.32
1.0
3.2
Phencyclidine (mg/kg, i.p.)

play a role, its effects may be overshadowed by those of ITI duration.

Pharmacological Manipulations

Ethanol. Ethanol did not increase the probability of risky choice except in a few isolated instances. Rather, risky choice decreased if possible, usually in a dose-related manner, regardless of whether ITI was 20 or 80 s and regardless of whether baseline risky choice was less than or greater than 50%.

Changes in risky choice occurred independently of changes in rate of trial completion. Rate of trial completion in the 20-s ITI condition was decreased by one or more ethanol doses, compared to the effects of vehicle, for all rats. That is, latency to complete a trial increased. In terms of magnitude of effect, though, rate of trial completion decreased 50% or more at any dose only in a minority of rats. Rate of trial completion in the 80-s ITI condition was affected less by ethanol: It was decreased by one or more ethanol doses in only half the rats, and rate of trial completion increased after two ethanol doses in another rat.

Ethanol does have caloric value, which could be seen as making it more likely that rate of trial completion would decrease in the 20-s versus the 80-s ITI condition because of the more positive energy budget in the 20-s than the 80-s ITI condition. Some or all of the rate decrease likely was due to the sedative effects of the higher doses, however, because the rats showed clear sedative and myorelaxant effects upon removal from the chamber (e.g., they moved slowly and were limp). Although ethanol has increased responding under FR schedules of food reinforcement, it most often increased periods of pausing (i.e., decreased response rate) under differential-reinforcement-of-low-rate (DRL) schedules (review in McMillan & Leander, 1976). The contingencies of the present study and those of a DRL schedule are alike in requiring a single response for reinforcer delivery after an actual or "contingent" S^{Δ} (negative stimulus) interval and in the fact that increasing rate of responding does not increase rate of reinforcement, which is true of FR schedules.

Phencyclidine. Phencyclidine did not increase risky choice. During the 20-s ITI condition, PCP did not affect risky choice compared to baseline or the effects of vehicle in the majority of rats. In the 80-s ITI condition, risky choice decreased, if possible, after at least one higher dose in the majority of rats.

Rate of trial completion was affected by PCP in all rats under the 20-s as well as the 80-s ITI condition, which confirms that the PCP doses given were behaviorally active. All PCP doses both increased or decreased rate of trial completion in half or more of the rats in both ITI conditions.

In rats, the effects of PCP primarily have been studied under an FR schedule of food reinforcement in the context of a drug-discrimination procedure, and response rates have been decreased (e.g., Beardsley & Balster, 1988). Studies of schedule-controlled behavior, including matching-to-sample and repeated-acquisition procedures in monkeys and pigeons, reported only decreases in response rates after PCP injections (Bergman, Hassoun, & Schuster, 1985; Chait & Balster, 1978; McMillan, Li, & Snodgrass, 1998; Thompson, Mastropaolo, Winsauer, & Moerschbaecher, 1986; Wenger, Hudzik, Moore, & Wright, 1996). In the mouse, however, in which the response was to break a light beam onto a photocell under a multiple FR fixed-interval (FI) schedule, PCP increased rates of FI responding at doses that only decreased rates of FR responding; these effects were seen as rate dependent (Wenger & Dews, 1976).

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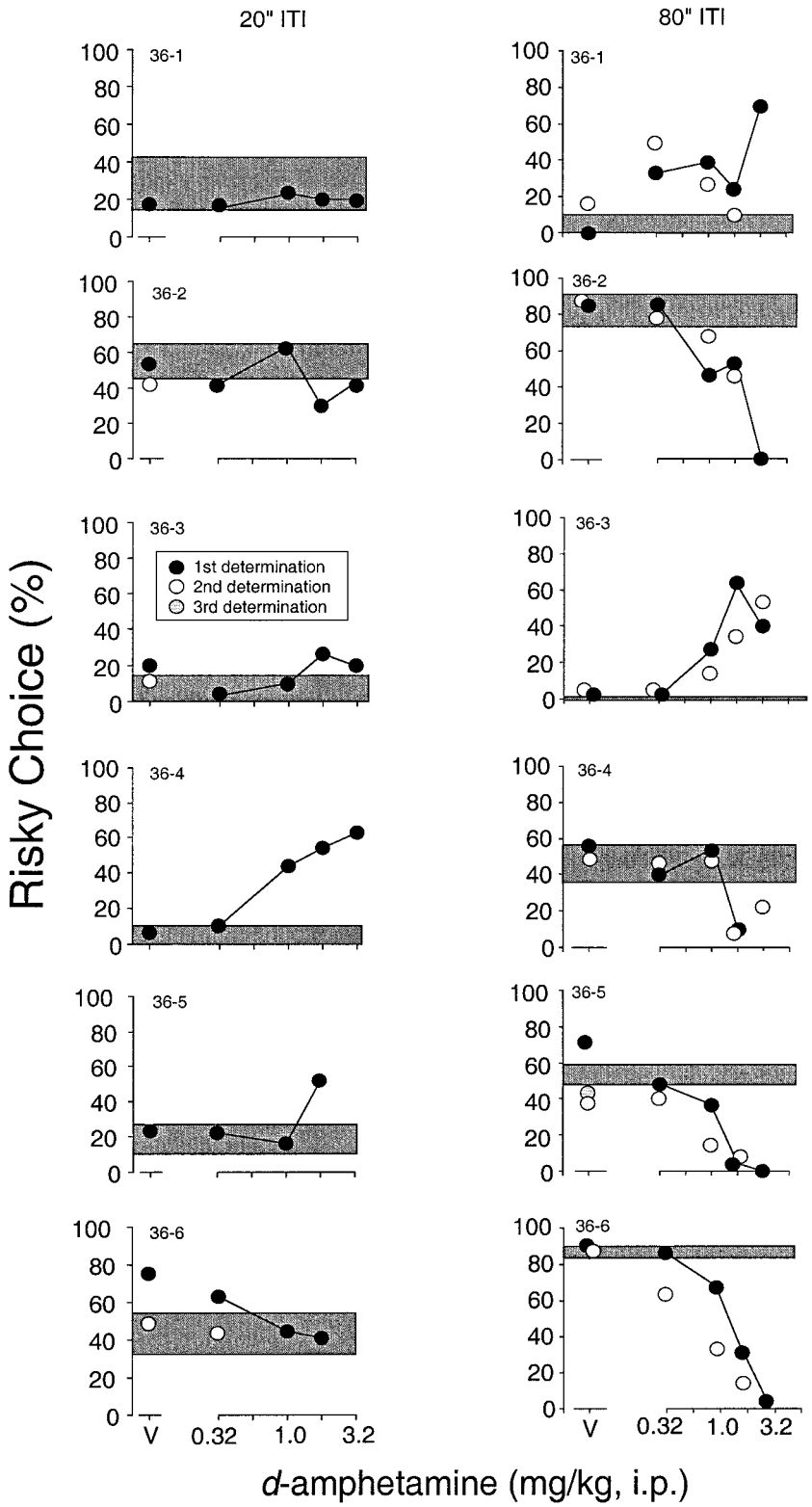
Fig. 7. Percentage of risky choices under a concurrent FR 1 FR 1 schedule of food delivery as a function of dose of phencyclidine (PCP) or its vehicle (V) administered by intraperitoneal (i.p.) injection when the ITI was 20 s (left column) and when it was 80 s (right column). Rats 36-5 and 36-1 were not studied under the 20-s and 80-s ITI conditions, respectively, due to scheduling constraints in proceeding to the next experimental condition. The shaded area in each panel encompasses the range of percentages of risky choice during the last five sessions prior to beginning drug testing in each ITI condition. Each point represents a single session, and the lines connect the first occasion on which the effects of the dose were determined. When no choice trials were completed, no point was plotted; but whether any forced trials were completed, and other data, can be seen in Tables 4 and 5 for the 20-s and 80-s ITI conditions, respectively.


20" ITI
80" ITI
36-1
36-2
36-3
36-4
36-5
36-6
1st determination
2nd determination
3rd determination
Risky Choice (%)
V
0.32
1.0
3.2
d-amphetamine (mg/kg, i.p.)

d-*Amphetamine*. The effects of *d*-amphetamine on risky choice appeared to be related to the relative baseline probability of risky choice. When baseline risky choice was 20% or less, regardless of the ITI, *d*-amphetamine increased risky choice. When baseline risky choice was 20% to 60% in the 20-s ITI condition, *d*-amphetamine did not systematically affect it. In the 80-s ITI condition, however, if the 20% to 60% range represented a relative increase in risky choice from the 20-s ITI condition for a given rat, then *d*-amphetamine decreased percentage of risky choice. When baseline risky choice was greater than 50% to 60%, only dose-dependent decreases in risky choice were observed.

Rate of trial completion was increased by the lowest dose of *d*-amphetamine in 5 of the 6 rats at the 20-s ITI, and the dose–response relationship for each rat was an inverted U-shaped function of dose. In the 80-s ITI condition, in which rate of trial completion after vehicle injections was higher for all rats than it had been after vehicle injections in the 20-s ITI condition, rate of trial completion was not increased consistently at the lowest *d*-amphetamine dose. The dose–response relationship in the 80-s ITI condition was an inverted U-shaped function of dose for most rats, however, but it was shifted to the right of the one at the 20-s ITI.

The present results on rate of trial completion after *d*-amphetamine are consistent with the literature on the rate-dependent effects of amphetamines in a variety of species (Dews & Wenger, 1977). That is, when the rate of making a particular response is low (but not zero), regardless of whether it is in a one- or two-choice situation, amphetamine tends to increase it at some doses. When the rate of a response is high, then amphetamine is likely to decrease it. The rate-dependency literature for amphetamines has been seen as dealing largely with rates of free-operant responding rather than with rates of trial completion. Because postreinforcer timeouts often were employed in these studies, however, rate of trial completion in the present study is not outside the realm of data for which a prediction of rate-dependent effects of amphetamine could be made. The contingency of the present study merely represents an extreme in terms of schedule value (i.e., FR 1 timeout 20 s, and FR 1 timeout 80 s).

The effects of *d*-amphetamine on risky choice itself (i.e., that a low percentage of risky choice would be increased and a high percentage decreased) are somewhat novel in terms of an extension of the predictions of rate dependency. However, even this measure is not inimical to ''rate'' dependency if we remember that Skinner (1953) favored response rate, a summary measure of response frequency, as a primary dependent variable because it gives a basis by which to predict the probability of a response. Thus, after low or intermediate doses of *d*-amphetamine, a low probability of responding on the risky lever tended to increase, whereas a somewhat higher probability was either unchanged or decreased; when responding on the risky lever was most probable, *d*-amphetamine decreased this probability.

Conclusion

When feeding was restricted to a maximum 90-min period each day, rats given a choice between a smaller, certain amount of food per trial and a larger but less certain amount of food per trial were risk averse. Because the amount of food obtained and the body weights maintained indicated that rats were on a positive energy budget under this condition, this outcome is consistent with the literature on risk-sensitive foraging (Kacelnik & Bateson, 1996). Increasing the FR resulted in

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Fig. 8. Percentage of risky choices under a concurrent FR 1 FR 1 schedule of food delivery as a function of dose of *d*-amphetamine or its vehicle (V) administered by intraperitoneal (i.p.) injection when the ITI was 20 s (left column) and when it was 80 s (right column). The shaded area in each panel encompasses the range of percentages of risky choice during the last five sessions prior to beginning drug testing in each ITI condition. Each point represents a single session, and the lines connect the first occasion on which the effects of the dose were determined. When no choice trials were completed, no point was plotted; but whether any forced trials were completed, and other data, can be seen in Tables 4 and 5 for the 20-s and 80-s ITI conditions, respectively. (In both ITI conditions, 5.6 mg/kg, not shown, was studied. All rats failed to respond in the 20-s condition; only Rat 36-3 responded in the 80-s ITI condition.)

rats becoming more risk averse, if possible, which is inconsistent with risk-sensitive foraging theories (Kacelnik & Bateson) and with application of the unit price analysis to the probabilistic choice situation (Hursh et al., 1988). The fact that the energy budget remained positive under these conditions may have been the strongest determinant of this failure to become more risk prone, but few manipulations of response requirement have been carried out with any species. On the other hand, increasing ITI markedly increased risky choice in most rats, which was concomitant with, but not necessarily a function of, a decrease in number of pellets and body weight as ITI increased. Because previous data on decreasing trials per session indicated either no change or greater risk aversion, the effect of the ITI increase, and thus the decrease in reinforcement density, apparently overrode the effect of fewer trials per session.

Contrary to a prevalent belief and some data that ethanol, PCP, and amphetamines increase risk taking in humans (e.g., Fromme, Katz, & D'Amico, 1997), only *d*-amphetamine increased risky choice in the present procedures. Even the increases in risky choice produced by *d*-amphetamine, however, seemed to be strongly a function of the baseline probability of risky choice in a direction opposite to what might be predicted for a human. That is, low probability of risky choice was increased by *d*-amphetamine, but a high probability of risky choice was decreased by *d*-amphetamine. Across drugs, changes in risky choice were seen to be independent of changes in rate of trial completion; in some cases, the occurrence of rate effects confirmed behavioral activity on the range of doses at which no effect on risky choice was observed.

The present procedure, initially introduced by Hastjarjo et al. (1990), may be particularly useful for more systematic study of parameters that affect risk-sensitive foraging in the rat. As noted above and emphasized by Kacelnik and Bateson (1996), much of that research has been conducted using birds; and the generality of several findings await investigation in other species.

The results of systematic manipulation of behavioral variables in risk-sensitive foraging research and those of the present study have important implications for laboratory models of risk taking in humans. That is, they make clear that risk taking may be studied productively as behavior that is a function of environmental variables. It increases or decreases as a function of constraints on reinforcer availability. Such a view may be contrasted with those that see risk taking as a trait or state. Further investigation of the effects of psychoactive drugs in the context of parametric changes in risky choice procedures may reveal drug–behavior interactions related to probabilistic reinforcers that are of both heuristic and applied value.

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