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FOOD-DEPRIVATION LEVEL ALTERS THE EFFECTS OF MORPHINE ON PIGEONS' KEY PECKING

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Four pigeons pecked response keys under a multiple fixed-ratio 30 fixed-interval 5-min schedule of food presentation. Components alternated separated by 15-s timeouts; each was presented six times. Pigeons were maintained at 70%, 85%, and greater than 90% of their free-feeding weights across experimental conditions. When response rates were stable, the effects of morphine (0.56 to 10.0 mg/kg) and saline were investigated. Morphine reduced response rates in a dose-dependent manner under the fixed-ratio schedule and at high doses under the fixed-interval schedule. In some cases, low doses of morphine increased rates under the fixed-interval schedule. When pigeons were less food deprived, reductions in pecking rates occurred at lower doses under both schedules for 3 of 4 birds compared to when they were more food deprived. When pigeons were more food deprived, low doses of morphine increased rates of pecking in the initial portions of fixed intervals by a greater magnitude. Thus, food-deprivation levels altered both the rate-decreasing and rate-increasing effects of morphine. These effects may share a common mechanism with increased locomotor activity produced by drugs and with increased drug self-administration under conditions of more severe food deprivation.

Key words: morphine, fixed-interval schedules, fixed-ratio schedules, food deprivation, key peck, pigeon

The effects of drugs on behavior are altered in several ways by level of food deprivation. The rate-decreasing effects of higher doses of psychomotor stimulants are lessened with increasing deprivation (Cole, 1967; Gollub & Mann, 1969; Hughes, Pitts, & Branch, 1996; Samson, 1986; Schaal & Branch, 1992; Schaal, Miller, & Odum, 1995). Increased food deprivation also has been shown to enhance the rate-increasing effects of low doses of cocaine (Schaal et al., 1995). Furthermore, across a wide variety of pharmacological classes, food-deprived subjects self-administer more drug than do subjects that are not food deprived (e.g., M. E. Carroll, 1985a, 1985b; de la Garza, Bergman, & Hartel, 1981; Meisch & Kliner, 1979; Meisch & Thompson, 1973, 1974; Papasava & Singer, 1985; Takahashi & Singer, 1979; see M. E. Carroll & Meisch, 1984, for a review).

Increases in drug self-administration due to food deprivation have been interpreted to reflect increases in the reinforcing efficacy of drugs (M. E. Carroll & Meisch, 1984; M. E. Carroll & Stotz, 1983; M. E. Carroll, Stotz, Kliner, & Meisch, 1984; Kliner & Meisch, 1989; Thompson, 1984; see M. E. Carroll, 1996, for a recent interpretation in terms of behavioral economics). For example, M. E. Carroll et al. (1984) investigated self-administration of phencyclidine (PCP) or pentobarbital when monkeys were food deprived and food satiated. The monkeys self-administered larger amounts of drug at the highest doses tested when they were food deprived than when they were satiated. The authors concluded that changes such as these may indicate that the drugs serve as more effective reinforcers when subjects are food deprived.

It is possible, however, that increases in drug self-administration with more severe food deprivation are due at least in part to changes in the way drugs affect the rate of ongoing behavior, regardless of the event that maintains that behavior. Although the increase in drug self-administration with more

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severe levels of food deprivation is likely to have multiple contributing causes, Schaal and Branch (1992) suggested that this effect may be due in part to the decreased ability of large doses of drug to suppress response rates when subjects are more food deprived. Schaal and Branch examined the effects of cocaine on key pecking maintained by a fixed-ratio (FR) 30 schedule of food delivery when pigeons were maintained at 70%, 80%, and >90% of their free-feeding weights. Cocaine suppressed response rates at lower doses when the subjects were relatively less food deprived. Thus, increases in drug self-administration when subjects are more food deprived could reflect the decreased tendency for large doses of drug to suppress responding.

Other factors almost certainly play a role in increased drug self-administration with food deprivation. For example, M. E. Carroll and Stotz (1983) found the overall drug intake of monkeys responding on an FR schedule of *d*-amphetamine delivery was lower when the subjects were food satiated than when they were deprived. Response rates were highest at the lowest doses of drug when the subjects were food deprived, but response rates increased monotonically across dose when subjects were satiated. Although this effect suggests that food deprivation increased the reinforcing effectiveness of low doses of *d*-amphetamine, it may be that the high response rates were due, in part, to a food-deprivation-induced enhancement of the direct rate-increasing effect of self-administered *d*-amphetamine. In support of this suggestion, Schaal et al. (1995) showed that increases produced by low doses of cocaine (another psychomotor stimulant) in rates of pigeons' key pecking under a fixed-interval (FI) 5-min schedule were larger and more reliable when pigeons were maintained at more severe deprivation levels (i.e., 70% vs. 85% of free-feeding weight). Thus, the enhanced ability of low doses of drugs to increase response rates when subjects are more food deprived may also play a role in increases in drug self-administration produced by food deprivation.

The decreased ability of large doses of psychomotor stimulants such as *d*-amphetamine and cocaine to suppress rates of food-maintained behavior when subjects are more severely deprived is well documented (e.g., Cole, 1967; Gollub & Mann, 1969; Hughes et al., 1996; Samson, 1986; Schaal & Branch, 1992; Schaal et al., 1995). However, the effects of opioids on operant behavior under different levels of deprivation have received little investigation (but see Kelly & Thompson, 1988). By examining the effects of morphine on the key pecking of pigeons maintained at several levels of deprivation, the present study sought to explore the generality of the modification of both the rate-decreasing and rate-increasing effects of drugs by food deprivation.

Morphine is an opioid that commonly decreases the overall rate of behavior maintained by positive reinforcement. For example, Smith (1978) maintained pigeons' key pecking on a multiple FR 30 FI 5-min schedule of food delivery and found that morphine reduced response rates on both schedules in a dose-dependent manner. Decreases in rates of food-maintained behavior with acute morphine administration have been reported for rats (Rhodus, Elsmore, & Manning, 1974; Snell & Harris, 1982; Taskin, 1986), pigeons (Goldberg, Morse, & Goldberg, 1976; Heifetz & McMillan, 1971; Picker, Grossett, Sewell, Zimmermann, & Poling, 1982; Slifer, 1982; Wenger, 1980), and monkeys (Byrd, 1975; Goldberg et al., 1976; Katz & Goldberg, 1986; McKearney, 1974, 1980) across a variety of schedules of reinforcement. However, slight increases produced by low doses of morphine on response rates maintained by FI (e.g., Goldberg et al., 1976; McMillan & Morse, 1967; Thompson, Trombley, Luke, & Lott, 1970) as well as FR and variable-ratio (VR) schedules of food delivery (Thompson et al., 1970) have been reported. Large rate increases in behavior maintained by FI schedules were found by Byrd (1975) with chimpanzees as subjects. The effects of morphine on behavior maintained by FI schedules have been shown to be rate dependent: Low rates in the initial portion of the interval increased and high rates in later portions of the interval decreased with rats (e.g., Rhodus et al., 1974), monkeys (e.g., Katz & Goldberg, 1986; McKearney, 1974), and pigeons (e.g., Heifetz & McMillan, 1971; Katz & Goldberg, 1986) as subjects.

The present study investigated the effects of food deprivation and morphine administration on pigeons' key pecking maintained by a multiple FR 30 FI 5-min schedule of food presentation. The multiple FR FI baseline was

Table 1

Order of deprivation conditions, weight at each condition, sessions to stability, and sessions following attainment of stability (total sessions) in each condition for each pigeon.

Pigeon	Condition order	Body weight (g)	Sessions to stability	Total sessions
70% of free-feeding weight				
78	1	451	40	202
53	1	359	37	209
40	2	369	52	218
10	2	374	47	222
85% of free-feeding weight				
78	2	548	55	150
53	2	436	69	138
40	1	448	37	202
10	1	454	37	198
>90% of free-feeding weight				
78[a]	3	612	42	103
53[a]	3	487	34	176
40[b]	3	479	63	163
10[b]	3	486	33	137

[a] 95%.
[b] 91%.

employed because it generates, within session, a wide range of response rates that are often differentially affected by drugs. The effects of acute morphine administration on key pecking were determined at three levels of food deprivation: 70%, 85%, and >90% of free-feeding weight.

METHOD

Subjects

Four adult male White Carneau pigeons with previous exposure to cocaine and to a multiple FR FI schedule of food reinforcement (Schaal et al., 1995) were used as subjects. Free-feeding weights were determined prior to the previous study. Pigeons experienced daily sessions without drug administration for a minimum of 2 months (range, 2 to 5) after completion of the prior experiment. Pigeons were maintained at different body weights through feedings that typically occurred within 15 min of the end of sessions. Absolute weights for each pigeon at each deprivation level are shown in Table 1. When not in experimental sessions, pigeons were individually housed in a temperature-controlled colony under a 12:12 hr light/dark cycle and were allowed free access to water and digestive grit. Sessions were conducted during the light portion of the cycle.

Apparatus

Four custom-made experimental chambers, constructed of wood with aluminum front panels, were used. The internal dimensions of each chamber were 33 cm across the front panel, 31 cm from the front panel to the back wall, and 37.5 cm from the floor to ceiling. Three plastic response keys (2.1 cm diameter) on the front panels were mounted 26 cm from the floor. The center key could be lit from behind with green or amber light and required a force of approximately 0.19 N to record a response. The side keys were dark, and pecks to these keys had no programmed consequences. A lamp (28 V 1.1 W) 7 cm above the center key served as a houselight. A rectangular aperture 16 cm below the center key provided access to a solenoid-operated food hopper filled with mixed grain. Extraneous sounds were masked by white noise and chamber ventilation fans. Contingencies were programmed and data were collected by an MS-DOS-based 80386 microcomputer using the Smart Cumulative Recorder® and an 80486 microcomputer, programmed under Medstate Notation® (MED Associates, Inc. & Tatham, 1991), located in an adjacent room.

Procedure

Experimental sessions were conducted 7 days a week at approximately the same time each day. Due to the pigeons' previous history, no pretraining was necessary. Two pigeons (78 and 53) were maintained at 70% of their free-feeding weights, and 2 others (40 and 10) were maintained at 85% of their free-feeding weights. All pigeons responded under a multiple FR 30 FI 5-min schedule. Reinforcement consisted of 4-s access to the food hopper. During hopper presentations, the aperture was lit with white light, and the houselight and keylight were extinguished. Ten minutes after pigeons were placed in the darkened chamber, the session began with the houselight lit and the center key lit amber. After 30 pecks on the center key, food was presented (i.e., FR 30 schedule), followed by a 15-s blackout in which all lights were extinguished and key pecks had no scheduled consequences. The houselight was then turned on, the center key was lit green, and

the first key peck after 5 min elapsed produced food (i.e., FI 5-min schedule). A 15-s blackout also followed food delivery on the FI schedule. This sequence was repeated six times before the session ended. If a reinforcer was not collected within 2 min for each FR component and within 8 min for each FI component, the component ended in a blackout and alternation continued.

Morphine (0.56, 1.0, 1.7, 3.0, 5.6, and 10.0 mg/kg) and its vehicle (0.9% saline) were administered in a mixed order for each pigeon. The same mixed order was used for all bodyweight conditions for a given pigeon, and dose–effect curves were determined completely before any dose was repeated. Pigeons were weighed prior to and after experimental sessions, and drug tests were not conducted if initial weights were not within 10 g of the appropriate weight for that deprivation condition. This event rarely happened. Morphine or vehicle tests were separated by at least three consecutive baseline sessions.

After completion of three or four tests of each dose at the initial weights, weights for Pigeons 78 and 53 were gradually increased from 70% to 85% of the free-feeding weights, and weights for Pigeons 40 and 10 were gradually decreased from 85% to 70% of the free-feeding weights. When overall response rates in both components were stable (i.e., showed no increasing or decreasing trends or extreme variability over the last 10 sessions), morphine and vehicle were tested as before. Finally, weights for all pigeons were increased to 95% of the free-feeding weights, and after response rates became stable, each dose of morphine and vehicle was tested two or three more times. Table 1 lists the number of sessions from the start of a weight change to the first administration of morphine for that weight (i.e., number of sessions in transition to the new weight and to stability of response rates at that weight) as well as the total number of sessions at a particular weight after drug testing began. For Pigeon 78, 5.6 and 10.0 mg/kg morphine were not tested at 95% of free-feeding weight because responding was largely suppressed at doses higher than 1.0 mg/kg. For Pigeons 40 and 10, rate of baseline responding decreased and became more variable after the first dose–effect curves at 95% of free-feeding weight. Their weights then were reduced to 91% of free-feeding weights, and testing continued when response rates and patterns were again stable. Results obtained at both weights were combined in data analysis.

Overall rates of key pecking and the temporal location, within the session, of each peck and each food presentation were collected daily. The session that immediately preceded a morphine or vehicle test session was designated a baseline control session.

Drug Administration

Morphine sulfate (obtained courtesy of the National Institute on Drug Abuse) was dissolved in sterile 0.9% saline and administered in a volume of 1.0 ml/kg of the body weight at 85% of the free-feeding weight. This procedure held constant the absolute amount of morphine that each pigeon received across the deprivation conditions. The actual doses administered thus varied slightly across deprivation conditions (i.e., pigeons received lower doses at higher body weights and higher doses at lower body weights). Morphine and vehicle were administered via intramuscular injection into the breast.

RESULTS

For all pigeons, both components controlled schedule-typical response rates and patterns. During the FR 30 component, a brief pause was followed by a high, steady rate until reinforcer delivery. During the FI 5-min component, response rate was close to zero early in the interval and increased as the interval elapsed.

Figure 1 shows mean overall response rates during the FR 30 and FI 5-min components for control sessions. In this and all subsequent figures, the number of sessions contributing to the control means for each pigeon at 70%, 85%, and >90% of free-feeding weights, respectively, were 23, 23, and 14 (Pigeon 78); 22, 21, and 16 (Pigeon 53); 24, 27, and 14 (Pigeon 40); and 21, 25, and 18 (Pigeon 10).

No systematic changes in mean control response rates occurred across pigeons during the FR component as a function of deprivation condition. For Pigeons 53 and 10, there were no differences in mean control rates across deprivation conditions. For Pigeon 78, the mean control rate increased with increases in

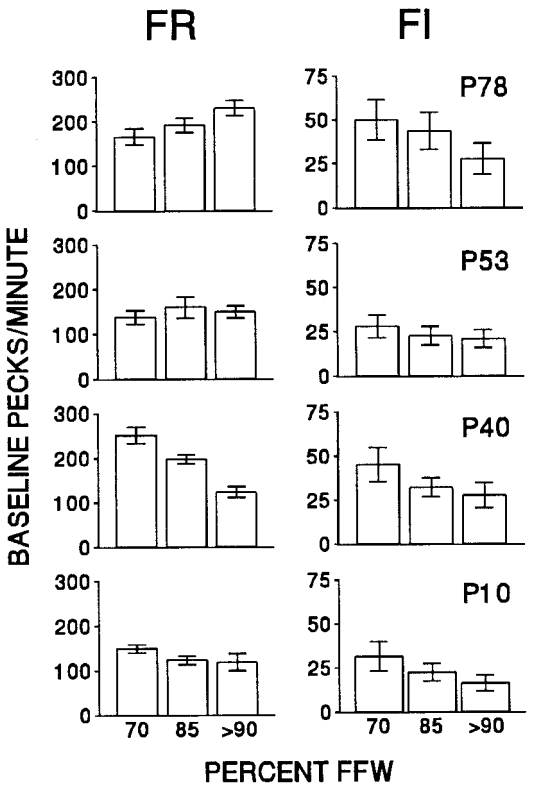

Fig. 1. Mean overall control rates (see text) under the FR 30 (left panels) and FI 5-min (right panels) schedules of food delivery for each pigeon at weights corresponding to three different percentages of free-feeding weight (FFW). Vertical bars show one standard deviation above and below means.

body weight, whereas for Pigeon 40, the mean control rate decreased with increases in body weight. The large degree of overlap between mean rates at each body weight and the unsystematic nature of changes across pigeons make it difficult to conclude that food-deprivation level affected mean control rates in an important manner during the FR component. During the FI component, mean control response rates decreased with increases in body weight for each pigeon. However, substantial overlap of control rates at each weight and the generally small magnitude of the differences across means make it difficult to conclude that food-deprivation level substantially altered mean FI control response rates.

Figure 2 shows the effects of morphine on responding expressed as percentages of the control response rates during the FR 30 and FI 5-min components for each pigeon at each deprivation level. Response rates for each determination of each dose at each body weight were divided by the mean of rates in all control sessions at that deprivation condition to yield the rate as a percentage of control rate; these values then were averaged. The saline vehicle had little substantial or systematic effect on response rates. Overall rates of pecking maintained by the FR schedule remained largely unaffected at the lowest doses, but decreased in a dose-dependent manner with higher doses. In general, the dose at which rates decreased was higher as food-deprivation level increased. The magnitude of these differences was largest for Pigeon 78. In some cases, there is overlap between dose–effect curves at different body weights; for Pigeons 40 and 53, differences in response rates between deprivation conditions in the FR component were minimal.

When Pigeon 40 was maintained at a weight higher than 90% of its free-feeding weight, response rates during the FR component increased relative to control with lower doses of morphine. Inspection of cumulative records (not shown) for Pigeon 40 revealed that extended pausing occurred prior to the start of responding during the FR component under the highest body weight. The increases in response rates with lower doses of morphine at the highest body weight were due to the elimination of this extended pausing.

The conclusions about how body weight alters the relation between morphine and response rate in the FR component would have been similar if they had been based on absolute response rates (not shown) instead of percentage of control rate. For Pigeons 53 and 10, dose–effect curves calculated as percentage of control rate differed little in shape from those of absolute rates because control rates at the different body weights were very similar (see Figure 1). For Pigeon 78, the mean control rate increased as deprivation level increased, and the dose–effect curves at each body weight overlapped less than those for absolute rates. For Pigeon 40, the mean control rate decreased as deprivation level increased, and the dose–effect curves at each body weight overlapped more than those for absolute rates.

The right panels of Figure 2 show that response rate maintained by the FI schedule of-

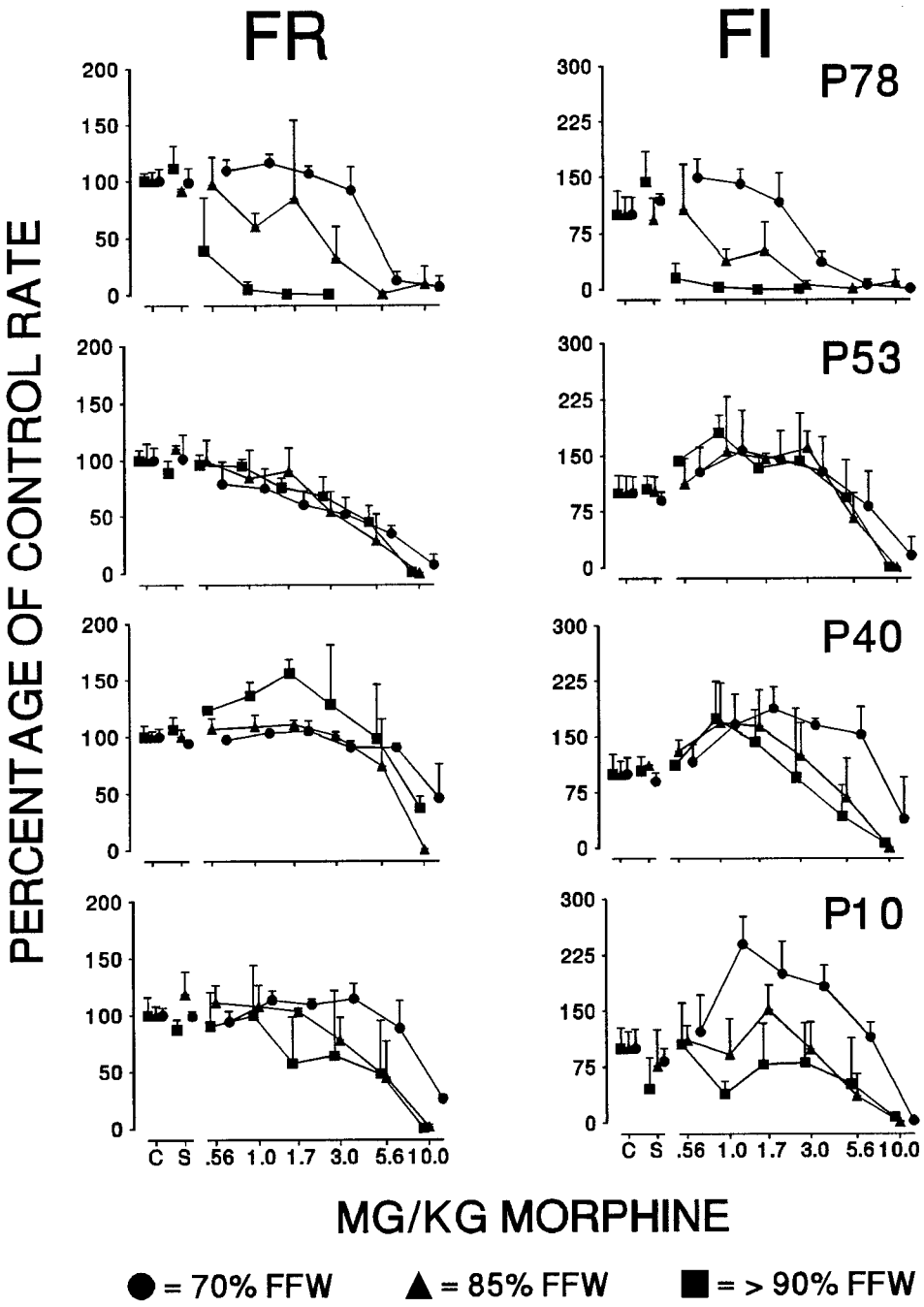

Fig. 2. Effects of morphine on rates of pecking expressed as percentages of control rate (see text for details) under the FR 30 (left panels) and FI 5-min (right panels) schedules of food delivery for each pigeon at weights corresponding to three different percentages of free-feeding weight (FFW). Unconnected points show mean rates for all control sessions (C) and determinations of saline (S). Lines connect points showing mean rates for at least two determinations of each dose at each body weight. Points are plotted above the actual dose of morphine received at each body weight (i.e., milligrams of morphine administered were divided by the body weight for that deprivation condition). Vertical bars represent one standard deviation above means. In some cases, the variability around a point is encompassed by the point.

ten increased, then decreased, as a function of dose, particularly when pigeons were maintained at 70% of free-feeding weight. Usually, the more extreme the level of deprivation, the higher the dose of morphine required to decrease FI rates. For Pigeon 78 at 95% of free-feeding weight, response rates during the FI component were suppressed at even the lowest dose of morphine. As for the FR component, in some cases there was overlap between dose–effect curves at different body weights; for Pigeon 53, there were no systematic differences in the effects of morphine on response rates during the FI component as a function of deprivation conditions. The mean of FI control response rates decreased for each pigeon as body weight increased (see Figure 1), and the dose–effect curves expressed as percentages of control rate overlapped more at the different levels of deprivation than those for absolute rates (not shown).

Figures 3 through 6 show response rates during successive 10ths (i.e., 30-s periods) of the FI 5-min schedule for Pigeons 78, 53, 40, and 10, respectively. Each point represents the mean rate per 10th (collapsed across the six FI components during sessions) averaged for control sessions and for sessions preceded by morphine administration. The pecks that produced reinforcement and the time after the interval elapsed until those pecks produced reinforcer delivery were not included in the calculations.

With few exceptions, mean control response rate increased across the interval at all body weights. Low doses of morphine typically increased the low mean response rates that occurred early in the interval. At higher doses, the higher mean rates during the latter part of the interval decreased compared to control rates. The increases in response rate early in the interval tended to be more pronounced at 70% of free-feeding weight than at higher body weights, and the decreases in response rates later in the interval typically became greater as body weight increased. These effects are most apparent for Pigeons 78 (Figure 3) and 10 (Figure 6) and least apparent for Pigeons 53 (Figure 4) and 40 (Figure 5).

Figure 7 allows assessment of the rate-dependent effects of morphine as a function of body weight relative to control rate. Mean rates following morphine administration at each dose at each body weight within each 10th of the FI (shown in Figures 3 through 6) were divided by control rates in the corresponding 10th of the interval for that body weight, multiplied by 100, and plotted on logarithmic axes as a function of mean control rate during the corresponding 10th of the interval. The effects of the lowest and highest doses are not shown because rates were largely unaffected at 0.56 mg/kg morphine and rates were largely uniformly suppressed at 10.0 mg/kg for most pigeons. The effects of 5.6 mg/kg morphine are not shown for Pigeon 78 because this dose was not tested at 95% of free-feeding weight.

Typically, low rates early in the interval increased and high rates later in the interval were either unaffected or decreased relative to control following morphine administration. Rate-decreasing effects were more pronounced for each pigeon as the dose of morphine increased. Possible modifications of the degree of these effects by food deprivation may be detected in various ways in Figure 7. First, because results are plotted against control rate, points above a given value on the *x* axis show the effect of morphine on the same control rate at different deprivation levels. With more severe food deprivation, rates following morphine administration were often shifted up compared to those obtained at less severe deprivation levels. Furthermore, the slopes and *y* intercepts of the regression lines fit to data from different deprivation levels may be examined. Lines with the same slope and *y* intercept would indicate no changes in the rate-dependency functions. For Pigeons 78 and 10, the slopes of the functions were similar at different deprivation levels, but the *y* intercepts typically increased as body weight decreased. For Pigeons 53 and 40, changes were of smaller magnitude and less consistent. For example, for Pigeon 53 the functions obtained following 1.0 and 3.0 mg/kg morphine were indistinguishable. When the functions differed for these pigeons, however, it was always with an increase in *y* intercepts at the lowest body weight. In terms of rate-decreasing and rate-increasing effects, these results indicate that the level of food deprivation often changed the degree of both rate increases and rate decreases. Greater rate increases and smaller rate decreases frequently occurred with more severe food deprivation.

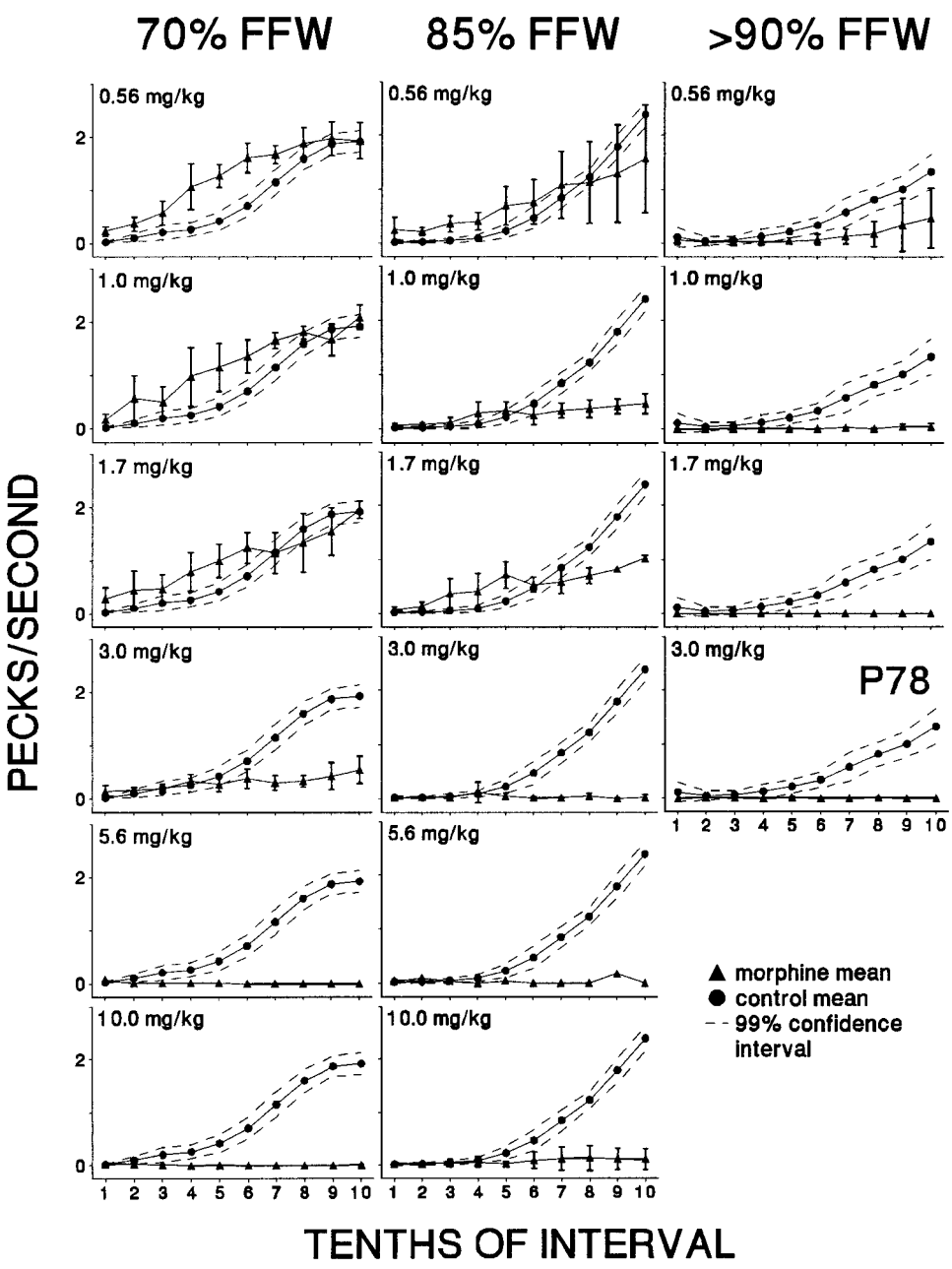

Fig. 3. Effects of morphine on rates of pecking during successive 10ths (30-s periods) of the FI 5-min schedule for Pigeon 78. Left, center, and right panels show rates at 70%, 85%, and >90% of free-feeding weight (FFW), respectively. Dashed lines above and below circles show 99% confidence intervals around control means. Vertical bars around triangles show one standard deviation above and below the means for each determination of each dose of morphine. In some cases, the variability around a point is encompassed by that point. Due to a computer error, data on which the analysis depends were unable to be analyzed for the second and third determinations of 5.6 mg/kg morphine at 70% of free-feeding weight; thus, only the effects of the first determination of this dose at that weight are shown.

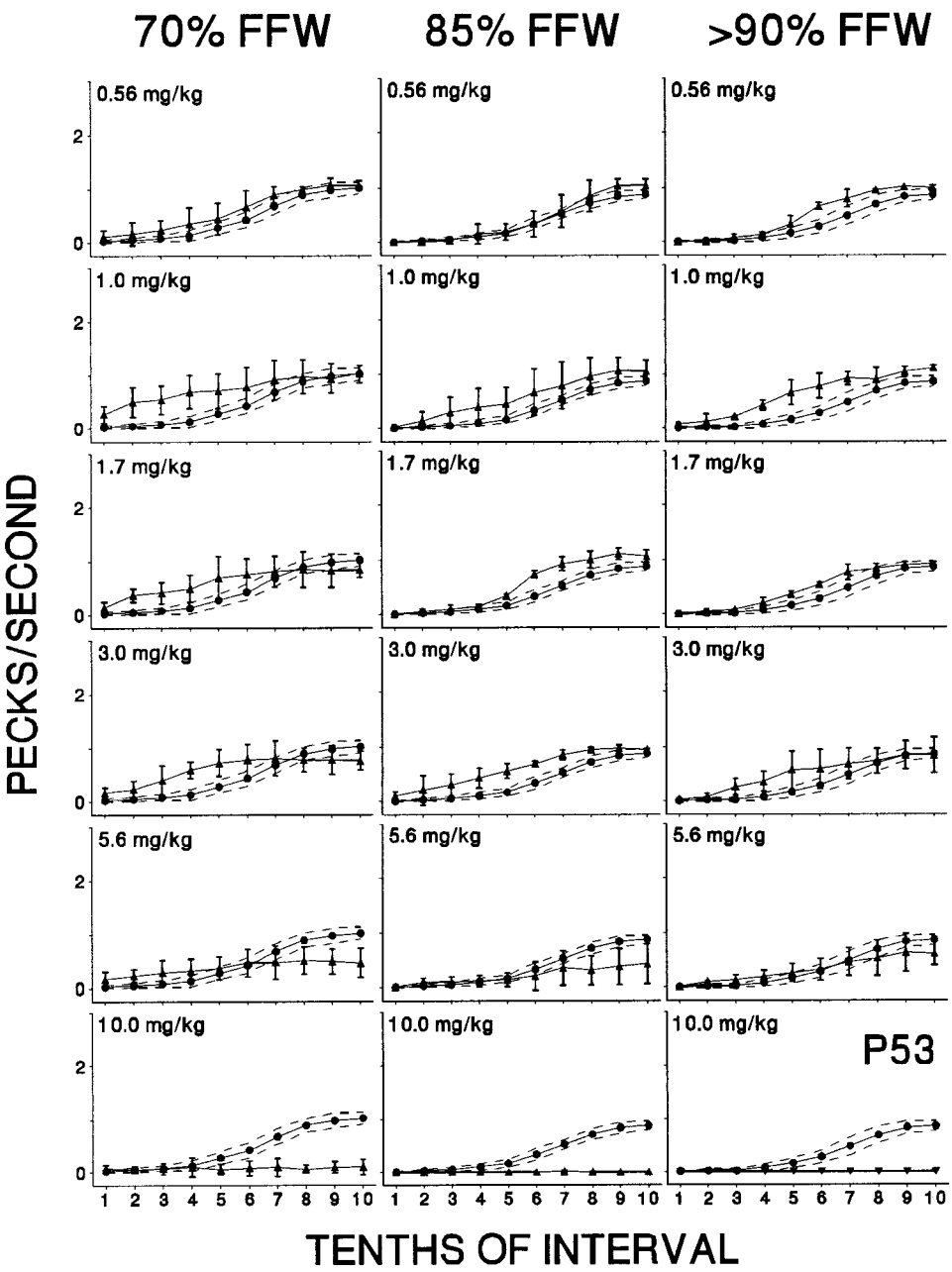

Fig. 4. Effects of morphine on pecking during successive 10ths of the FI 5-min schedule for Pigeon 53. Due to a computer error, data were unable to be analyzed for the first determination of 10.0 mg/kg morphine at 95% of free-feeding weight; thus, only the effects of the second determination of this dose at that weight are shown. Other details as in Figure 3.

DISCUSSION

The results of the present study are consistent with those from previous research on the effects of morphine on food-maintained operant behavior. In general, overall response rates decreased in a dose-dependent manner (cf. Smith, 1978). Increases in overall rate typically occurred only for rates maintained by the FI schedule and most clearly at the

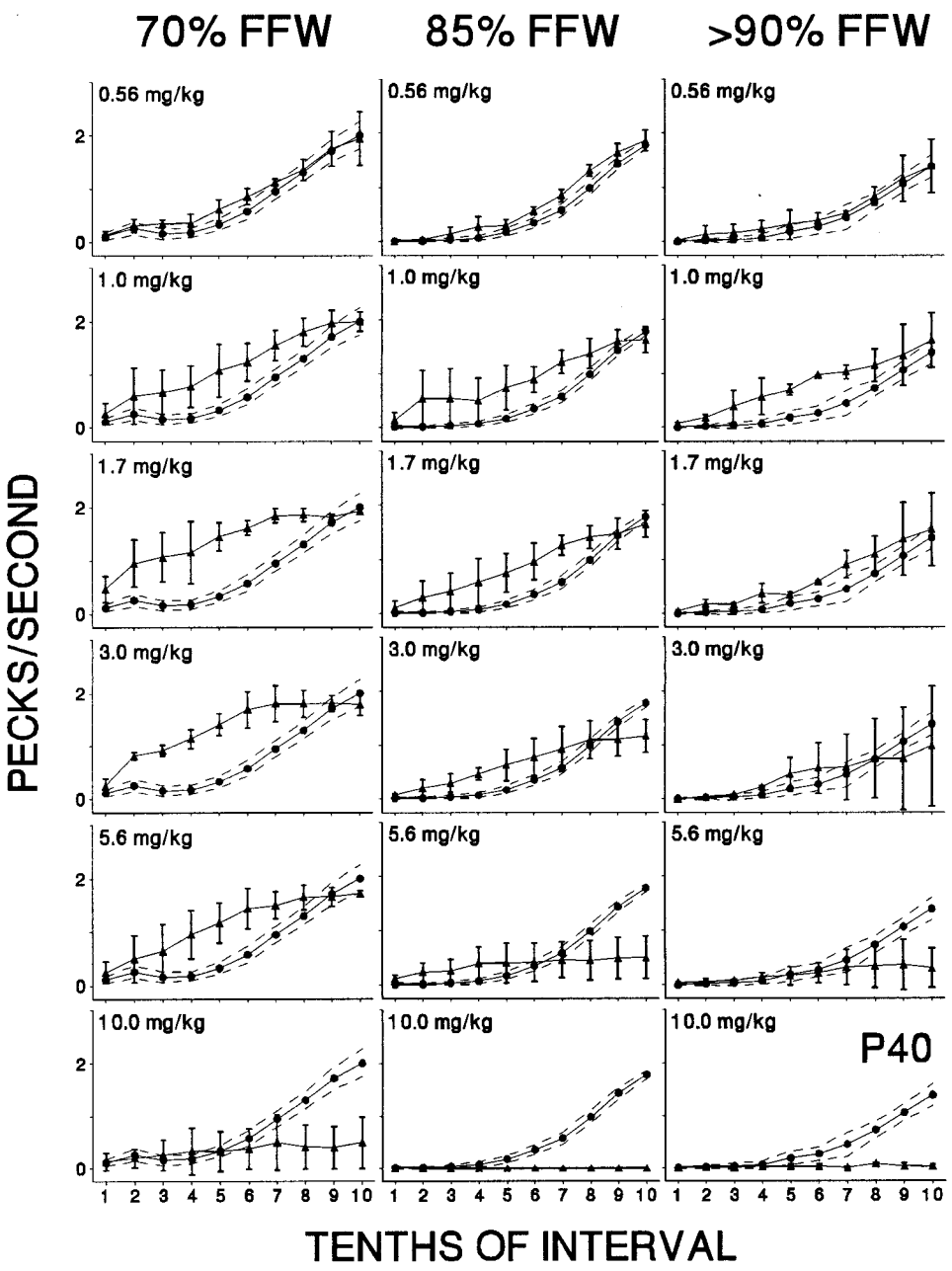

Fig. 5. Effects of morphine on pecking during successive 10ths of the FI 5-min schedule for Pigeon 40. Due to a computer error, data were unable to be analyzed for the third determination of 3.0 mg/kg at 70% of free-feeding weight; thus, only the effects of the first, second, and fourth determinations of this dose at that weight are shown. Other details as in Figure 3.

lowest body weight (cf. Kelly & Thompson, 1988, for methadone, another opioid). Furthermore, analysis of rates within the fixed interval showed that the effects of morphine were rate dependent: High rates decreased and low rates increased (cf. Heifetz & McMillan, 1971).

The dose of morphine that was needed to decrease overall rates of key pecking maintained by the FR 30 and FI 5-min schedules

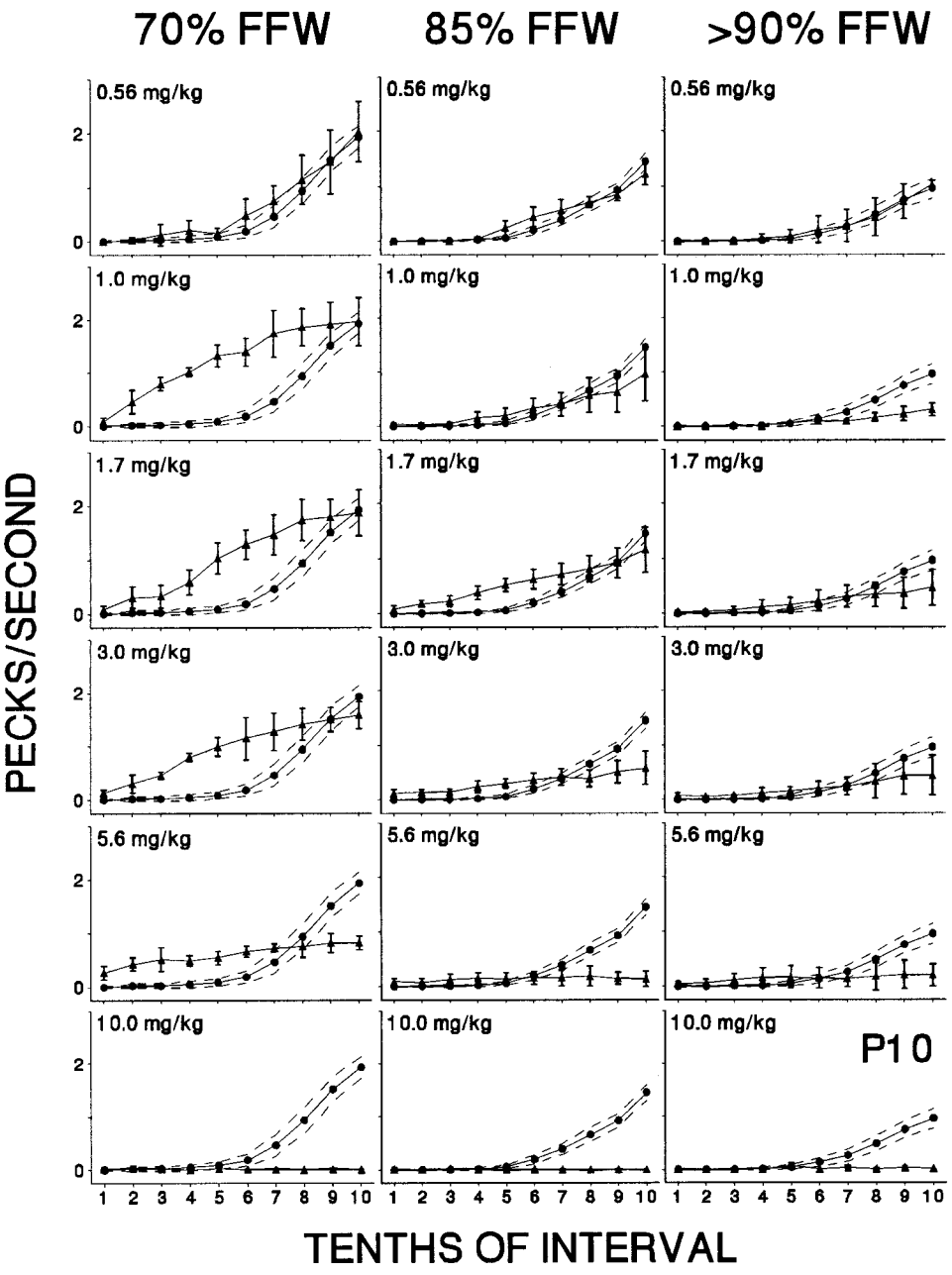

Fig. 6. Effects of morphine on pecking during successive 10ths of the FI 5-min schedule for Pigeon 10. Other details as in Figure 3.

was usually lower when the pigeons were relatively less food deprived. Similar effects have been found previously for methadone (Kelly & Thompson, 1988) and psychomotor stimulants (Cole, 1967; Gollub & Mann, 1969; Hughes et al., 1996; Samson, 1986; Schaal & Branch, 1992; Schaal et al., 1995). Increases in overall response rates on the FI 5-min schedule usually were more pronounced at the most severe level of food deprivation. Food-deprivation levels altered the effects of morphine on response rates within fixed in-

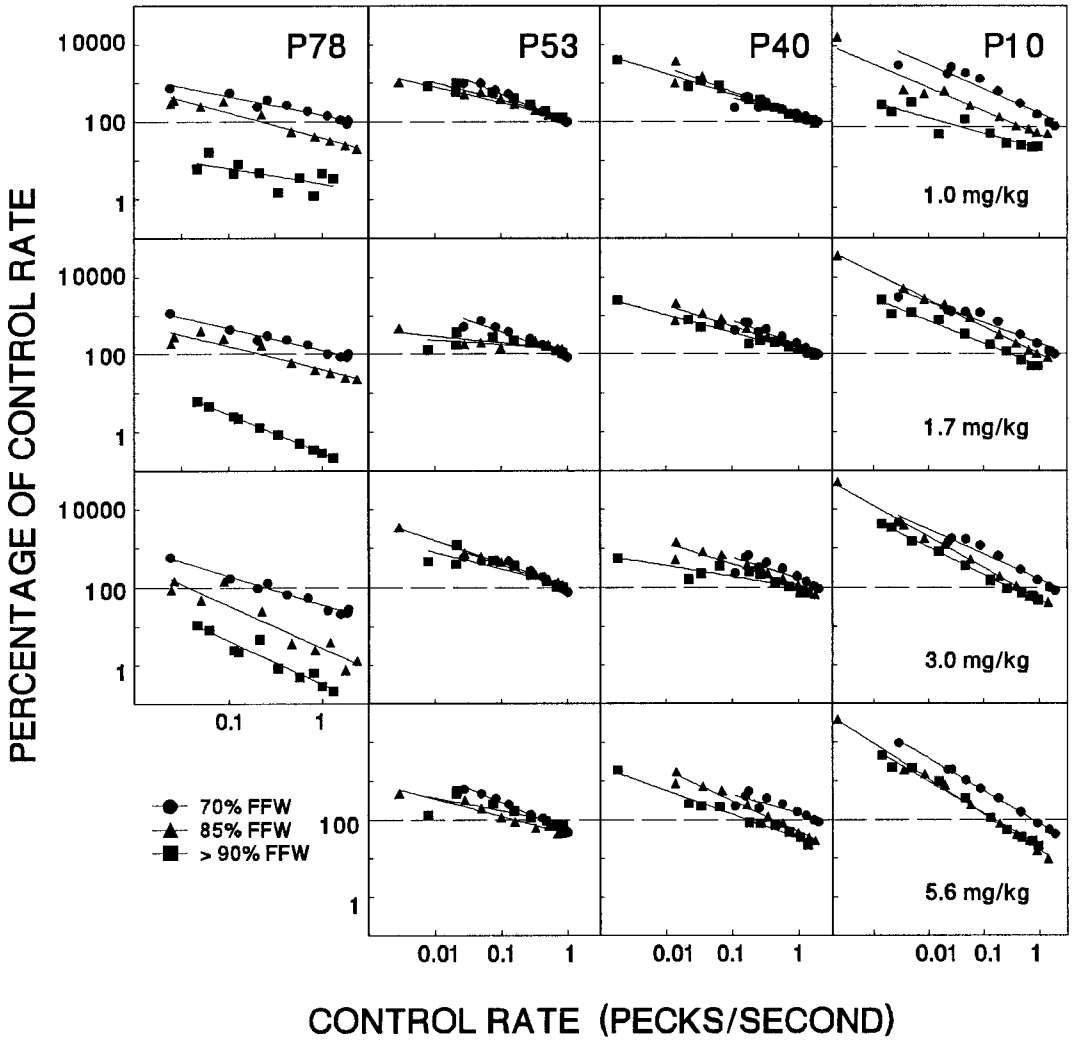

Fig. 7. Response rates within each 10th of the FI 5-min interval (i.e., successive 30-s segment) following administration of morphine for each of 4 pigeons (columns) at four doses of morphine (rows). The *x* axis shows control rate in each 10th, and the *y* axis shows percentage of control rate in the corresponding 10th following morphine administration. The dashed horizontal line indicates 100% of control rate (i.e., no change relative to control). Points above the dashed line represent rate increases, and points below the dashed lined represent rate decreases, relative to control rates. Circles, triangles, and squares depict rates at 70%, 85%, and >90% of free-feeding weight (FFW), respectively. Linear regression lines were fit by the method of least squares. Note that *x* axes are scaled for individual subjects. See text for details of calculations.

tervals as well. At lower body weights, rate increases during the initial part of the interval were more robust, and rate decreases during the later part of the interval were attenuated. Similar effects on behavior maintained by FI schedules have been obtained following administration of cocaine (Schaal et al., 1995) and methadone (Kelly & Thompson, 1988).

The present study thus provides evidence that both the rate-increasing and rate-decreasing effects of morphine were altered by food-deprivation level. There are at least two possible explanations for these effects that may be eliminated by these data. If, for example, the absolute amount of drug had not been held constant across body weights (i.e., if mg/kg had been held constant), then pigeons would have received less morphine at lower body weights, thus perhaps explaining the diminution of the rate-decreasing effects

of higher doses at lower body weights. Because the absolute amount of drug was fixed at that proportional to the 85% weight, in the present study the dose pigeons received actually increased with decreases in body weight. Thus, based on variations in dose alone, rates should have been suppressed more at lower body weights. Because the present study found that rates were suppressed more at higher body weights, it suggests that the reduced tendency of morphine to decrease rates with decreases in body weight is an effect that can overcome that of increases in dose.

A second possible explanation for these types of changes may be eliminated as well. A well-known finding in behavioral pharmacology is that drug effects frequently are related to the baseline rate of behavior (e.g., Dews, 1958; Dews & Wenger, 1977). Thus, if food-deprivation level were to systematically alter the baseline rate of behavior, changes in the effects of morphine could possibly be parsimoniously explained in terms of changes in baseline rate. This possibility can be ruled out on three grounds. First, the most common rate-dependent finding is that low rates increase and high rates decrease or are less affected. Because increasing food deprivation increased mean baseline rates during the FI (albeit to a small degree), a prediction based on the rate-dependency principle could suggest that increasing food deprivation should actually magnify the rate-decreasing effects of morphine. Because the higher baseline rates under more severe food deprivation increased more, rather than less, than the lower baseline rates under less severe food deprivation, the present results suggest that changes in the effects of morphine as a function of food-deprivation level can overcome those that could be predicted on the basis of differences in control rates.

A second reason that an explanation based on changes in control rates fails is that there were no systematic changes across pigeons in mean baseline rates in the FR component and only small systematic changes in mean baseline rates in the FI component, yet systematic changes in the effects of morphine on overall rates still occurred. Finally, if changes in the effects of morphine were only the result of differences in mean control rates, then the rate-dependency functions should superimpose, but in many cases they did not. It should be noted that the above arguments apply to the level of analysis of mean rates as conducted in the present experiment, and as such do not preclude the possibility that a more fine-grained aspect of control performance could be affected by body weight in a way that is related to the observed changes in the effects of morphine.

The results of the present study may have implications for the increase in drug self-administration commonly observed when subjects are food deprived (see also Schaal & Branch, 1992; Schaal et al., 1995). Food deprivation may enhance rate-increasing and attenuate rate-decreasing effects of self-administered drug, both of which may contribute to increased levels of drug consumption. However, such an interpretation cannot account for some findings in self-administration research. For example, M. E. Carroll (1985a) maintained the responding of monkeys on a second-order schedule that produced access to a fixed amount of PCP only at the end of the session. When subjects were food deprived, response rates prior to the delivery of drug were higher than when subjects were not food deprived. Such findings cannot be attributed to direct behavioral effects resulting from the interaction of food deprivation and drugs, because the effects occurred before the drug was self-administered. The present results do suggest, however, that alterations in the direct (as distinct from the reinforcing) effects of drugs due to food deprivation may play a role in increased drug self-administration under some circumstances.

Response-rate increases following administration of morphine (the present study) or cocaine (Schaal et al., 1995) at severe levels of deprivation may also be related to another effect of these drugs. It is well documented that morphine, cocaine, and amphetamine increase locomotor activity in rodents (e.g., Babbini & Davis, 1972; B. J. Carroll & Sharp, 1972; Funada, Suzuki, & Misawa, 1994; Kuczenski, Segal, & Aizenstein, 1991; Libri, Ammassari-Teule, & Castellano, 1989; Pulvirenti, Swerdlow, & Koob, 1989; Reith, 1986; Reith, Meisler, & Lajtha, 1985; Stone, Rudd, & Gold, 1990). Furthermore, the locomotor-activity-increasing effects of morphine and amphetamine are enhanced by increased food deprivation (Campbell & Fibiger, 1971; Deroche

et al., 1995; Deroche, Piazza, Casolini, Le Moal, & Simon, 1993). These parallel effects of food deprivation and drugs on both the locomotor activity of rodents and the operant key pecking of pigeons suggest a common behavioral mechanism. Specifically, drug-induced increases in locomotor activity and other behavior may be expressed as increases in the rate of well-learned performance in an operant chamber. In the absence of experimenter-programmed reinforcement contingencies, drug-induced motor activity takes several forms, including locomotion, exploration, grooming, and so on. Under some circumstances, a previous history may make it more likely that explicitly trained operant behavior predominates among those activities. Thus, increases in rates of key pecking following cocaine or morphine administration, and their alteration by food deprivation, may be outcomes of these drugs' general effects on locomotor activity.

In summary, parallel changes in behavior produced by level of food deprivation on the effects of drugs on food-maintained operant behavior, the effects of drugs on locomotor activity, and the rate of drug self-administration suggest that common mechanisms may be responsible. Of the interpretations offered thus far, none can account for all of the changes in behavior observed in the three situations. For example, changes in the direct rate-increasing effects of drugs on operant behavior do not explain why rates of drug self-administration increased prior to drug delivery (M. E. Carroll, 1985a). Similarly, changes in the reinforcing efficacy of drugs due to food deprivation do not explain why food deprivation enhanced drug-produced increases in operant key pecking maintained by food delivery (Kelly & Thompson, 1988; Schaal et al., 1995; the present study) or locomotor activity (e.g., Deroche et al., 1995). Perhaps it must suffice at this point to note that food deprivation modulates drug effects in several preparations and to suggest that an explanation that applies satisfactorily to all is wanting.

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