SPECIES DIFFERENCES IN TEMPORAL CONTROL OF BEHAVIOR

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Temporal control of rats' and pigeons' responding was analyzed and compared in detail on fixed-interval and fixed-time schedules with parameters of 30, 60, and 120 seconds. On fixed-time schedules, rats' responding decreased greatly or ceased, whereas pigeons continued to respond, especially on low schedule values. The running rate of responses (calculated by excluding the postreinforcement pause) was related to the duration of the preceding postreinforcement pause for rats but not for pigeons. Changes in response rate in successive segments of the interval were best described by normal curves. The relationship between midpoints of the normal curves and schedule value was a power function, with an exponent of less than one for pigeons but greater than one for rats. These differences could be explained in terms of a basic difference between the key-peck and lever-press responses, the two being differently affected by the response-eliciting properties of food.

Key words: temporal control, lever-press, key peck, postreinforcement pause, running rate, fixed interval, fixed time, rats, pigeons

In recent years, the observation that in some cases different species can be differently affected by the same learning conditions has given rise to the assertion that the principles and phenomena of operant and classical conditioning lack generality across species. One of the strong arguments, however, for the power of schedules of reinforcement as determinants of behavior is that their effects are orderly and replicable both within and across species (Morse, 1966; Skinner, 1959, 1968; Zeiler, 1977). Indeed, Sidman (1960) suggested that the adequacy of experimental control may be evaluated on the basis of whether behavior typical of the schedule in operation is reproduced, and that failure to replicate a finding within or between species is the result of an incomplete understanding of the controlling variables.

On the other hand, instances of species-specific behavior patterns, which apparently defy analysis in terms of traditional learning paradigms, have been extensively catalogued (Bindra, 1974; Bolles, 1972; Breland and Breland, 1961; Hinde and Stevenson-Hinde,

1973; Seligman, 1970; Shettleworth, 1972). Moreover, although the generality of schedule effects is well supported in the literature, there are some notable exceptions. On differential-reinforcement-of-low-rate (DRL) schedules pigeons do not distribute their key-pecking responses in time so as to match the schedule parameter in any degree of accuracy comparable to how rats distribute lever presses. This difference is particularly marked with schedule parameters of 20 sec and longer (Farmer and Schoenfeld, 1964; Harzem, Lowe, and Davey, 1975; Richardson and Loughhead, 1974; Staddon, 1965). One possible explanation is that pigeons differ from rats in ability to judge time intervals. If so, the two species would be expected to perform differently also on other time-related schedules, for example the fixed-interval (FI) schedule. Although this possibility has not been investigated in any detail, there is some evidence of such a difference. Killeen (1975) plotted pigeons' response rate as a function of time since the preceding reinforcement on different FI schedules, and fitted normal curves to the data points. Taking the midpoint of the normal curve as the point indicating the pigeon's judgement of the duration of the interval, he found that the relationship between these points of judgement and the duration of the fixed intervals was a power function with an

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exponent of 0.8. No similar function was found, however, for data obtained from rats, although this evidence was based on few data points.

Further evidence of a difference in the FI performance of the two species comes from a comparison of two other studies. In rats, increasing the magnitude of reinforcement increased both the duration of the postreinforcement pause and the running rate of responses (*i.e.*, the response rate calculated after excluding the postreinforcement pauses) (Lowe, Davey, and Harzem, 1974). In pigeons, the relationship between reinforcer magnitude and duration of the postreinforcement pause was the same, but the running rate was an inverse function of the magnitude of reinforcement (Staddon, 1970).

In view of the fact that a very large proportion of operant literature is based on studies of the key-pecking responses of pigeons and the lever-pressing responses of rats, and in the context of the growing interest in species-specific behavior, it seems important to analyze these differences more comprehensively and in detail. The present study was conducted for this purpose.

METHOD

Subjects

Eleven male hooded rats and 12 male mixed-breed pigeons, experimentally naive at the start of the experiment, were maintained at approximately 80% of their free-feeding weights.

Apparatus

Lehigh Valley Model 141-16 chambers, with the centre key illuminated, were used with pigeons, and Model 143-25 chambers, with only the left lever present, were used with rats. The reinforcer was 3-sec access to grain for pigeons and a 45-mg Noyes Pellet for rats. The experiment was controlled by solid-state logic units and the data were recorded and analyzed on a Nova 1200 computer.

Procedure

Three interval values were used: 30 sec, 60 sec, and 120 sec, a group of four rats and four pigeons being assigned to each value. The animals were first exposed to FI schedules, then to fixed-time (FT) schedules where the

delivery of the reinforcer at the end of each interval was independent of the subjects' responding, and finally to the original FI schedules. Each experimental session lasted until the subject received 40 reinforcements. Eighty daily sessions were conducted on first exposure to the FI schedule, 50 sessions on the FT schedule, and 40 further sessions on reintroduction of the original FI schedule. Inspection of the records showed that responding was stable before each schedule change.

RESULTS AND DISCUSSION

Figure 1 shows sample cumulative records obtained from one rat (11M) and one pigeon (11PN) in the last session of each phase of the experiment on the 30-sec condition. These records are representative of the performance of the other subjects in these conditions. The response patterns of the two animals were similar on first exposure to the FI 30-sec schedule, showing the pause-response sequence typical of animal performance on this schedule (Ferster and Skinner, 1957). When the schedule was changed to FT 30-sec, the rate and pattern of responding for the pigeon remained much the same, whereas responding ceased almost completely for the rat. When the schedule was returned to FI 30-sec, the rat's initial FI pattern of responding was recovered.

Representative cumulative records on the 60-sec conditions, for rat 5M and pigeon 5PN, are shown in Figure 2. For both animals, the response rate and patterning were similar on the FI 60-sec schedule. On the FT schedule, however, while there was a slight decline in response rate for the pigeon, the rat's responding ceased almost entirely and returned to its original form when the FI 60-sec schedule was reinstated.

Figure 3 shows cumulative records obtained on the last sessions of the 120-sec condition from rat 1M and pigeon 1PN. On the FT 120-sec schedule, both animals responded at a very low rate, there being few occasions when responding occurred in the course of the interreinforcement interval. On return to the FI 120-sec schedule, the pigeon's responding returned to its previous form on first exposure to this schedule. The rat's responding, however, did not return to its earlier form; there was an increase in the response rate, and

Fig. 1. Cumulative records of rat 11M and pigeon 11PN, from the last session on FI 30-sec, FT 30-sec, and re-exposure to FI 30-sec schedules.

the pause-response pattern occurred in many more intervals than in the FT 120-sec schedule.

Figure 4 presents data from all conditions of the experiment, showing the mean duration of the postreinforcement pause, the running rate, and the overall response rate for each subject on each schedule. Data are from the last four sessions on each schedule. In cal-

culating the mean postreinforcement pauses and the running rates, those interreinforcement intervals that did not contain at least one response were excluded. In every case, the response rate of rats declined markedly on all FT schedules, with poor recovery of FI 120-sec performance following exposure to the FT 120-sec schedule. There was little effect of the change to the FT schedules in pigeons

Fig. 2. Cumulative records of rat 5M and pigeon 5PN, from the last session on FI 60-sec, FT 60-sec, and re-exposure to FI 60-sec schedules.

on the 30-sec condition, some decline in responding on the FT 60-sec schedule, and a marked decline on the FT 120-sec schedule for three of the four birds in this group.

The decline in the response rate of pigeons, particularly on the FT 120-sec schedule agrees with earlier findings of a decrement in responding when an FT schedule of 120 sec or longer was introduced following performance on a comparable FI schedule (Shull, 1971; Zeiler, 1968, 1977). The present data indicate

that at shorter values of the FT schedules, pigeons' responding persists, this being in marked contrast to the performance of rats on the same schedules.

For both pigeons and rats, the durations of postreinforcement pauses were directly related to the duration of the scheduled interreinforcement interval. For rats, whether the delivery of reinforcement was contingent on responding had little systematic effect on the duration of those postreinforcement pauses

Fig. 3. Cumulative records of rat 1M and pigeon 1PN, from the last session on FI 120-sec, FT 120-sec, and re-exposure to FI 120-sec schedules.

Fig. 4. Overall response rate, running rate, and duration of postreinforcement pause on each schedule of each condition, for individual rats and pigeons. Data were averaged across the last four sessions of each schedule.

that did occur (bearing in mind that intervals in which no response occurred were excluded from calculation, not being counted as postreinforcement pauses). This was true also of pigeons on the 30-sec and 60-sec conditions, but on the FT 120-sec schedule there was an increase in duration of the postreinforcement pauses for all four birds. (Two of the rats on the FT 120-sec condition showed a similar increase in duration of postreinforcement pause when the schedule was FT). This contrasts with Shull's (1971) finding that the duration of the postreinforcement pause in pigeons was unaffected by a transition from an FI 120-sec schedule to an FT 120-sec schedule, although inspection of his data shows that in some

pigeons, duration of the postreinforcement pause increased.

Analysis of Fixed-Interval Performance

The data from the first exposure to the FI schedules were further analyzed to discover the nature of the relationship, if any, between the duration of the postreinforcement pause and the subsequent running rate within an interval. For each schedule, the postreinforcement pauses were placed in six categories according to their duration, each category representing successive sixths of the schedule parameter. The mean running rate following the pauses in each bin was then calculated.

Figure 5 shows running rate as a function of the postreinforcement pause duration for all subjects on each of the FI schedules. Data are from the last four sessions on each schedule. For all rats, the running rate was an increasing function of the postreinforcement pause, while for pigeons, no such relationship was evident. Thus, it appears that rats' response rate is sensitive to time-since-reinforcement, and that pigeons' responding is insensitive to this temporal variable.

One important question that arises is whether the duration of the postreinforcement pause affects responding throughout the running time (*i.e.*, time from the first response in an interval to the next reinforcement), or whether the effects are localized, being stronger in the early parts of the interval; that is, whether the response pattern is best described as break-and-run, where there is a rapid transition to a constant response rate, or as a scallop, involving a positive acceleration in responding as the interval progresses. To answer this question, the durations of individual interresponse times (IRTs) were analyzed in relation to the preceding postreinforcement pause duration. Figure 6 shows, for each subject, the mean duration of the first, sixth, and eleventh IRTs, which occurred following a postreinforcement pause, as a function of the duration of that pause. In the case of rats, the durations of the IRTs were inversely related to the duration of the preceding postreinforcement pause, and this was the case for all three IRT functions. For pigeons, there was evidence of a similar relationship for the first IRT, although this was not as consistent as with the rats, birds 6PN, 7PN, and 3PN being exceptions, and there was no systematic effect on the sixth and the eleventh IRTs. Shull and Brownstein (1970) also observed that in pigeons the duration of the postreinforcement pause does not affect the duration of the sixth and further IRTs.

For both rats and pigeons, there was an ordinal effect on IRTs, the first, sixth, and eleventh IRTs being successively shorter. This relationship was more marked following shorter postreinforcement pauses.

Thus, it appears that the response rate of rats is affected by temporal factors throughout an interreinforcement interval, specifically by the time elapsing since previous reinforce-

Fig. 5. Mean running rate as a function of the duration of the preceding postreinforcement pause, for individual rats and pigeons. Data are from the last four sessions of first exposure to each of the FI schedules.

ment. Pigeons, on the other hand, are not similarly sensitive to this variable (or at least not to the same degree, *cf.* Staddon and Frank, 1975). One implication of this is that a variable that increases the duration of the postreinforcement pause in both rats and pigeons, should also increase the running rate in rats, but not in pigeons. This is, in fact, the case when the magnitude of reinforce-

Fig. 6. Mean durations of the first (filled circles), sixth (crosses) and eleventh (plusses) IRTs following a post-reinforcement pause, as a function of the duration of that pause. The data are from the last four sessions of first exposure to each of the FI schedules.

ment is manipulated. Lowe *et al.* (1974), using rat subjects on an FI 60-sec schedule, found that increasing the concentration of the liquid reinforcer resulted in an increase both in the duration of the postreinforcement pause and in the running rate. With pigeons on the same schedule, however, Staddon (1970) found that when the duration of access to grain was increased, the duration of the post-reinforcement pause increased but the running rate was unaffected.

The data on FI performance were further analyzed in terms of local response rates in successive segments of a fixed interval. Figure 7 shows these rates of responding as a function of time since previous reinforcement. The data are averages (geometric means) across animals in each group taken from the last four sessions of first exposure to the FI schedules. Normal curves were fitted to these points with parameters as given in Table 1. These curves account for approximately 99.6% of the data variance and are similar

to those fitted by Killeen (1975) to the data of Catania and Reynolds (1968), and Dukich and Lee (1973). Catania and Reynolds used pigeons as subjects on FI 20-sec, 50-sec, and 120-sec schedules; rats were used by Dukich and Lee, on FI 60-sec and 120-sec schedules.

In Figure 8, the product of M and T , where T is the value of the fixed interval and M is the midpoint of the curve expressed as a proportion of the interval, has been plotted as a function of T ; multiplying M by T shows, for any given schedule value, where in the interval, in seconds, the midpoint of the response curve occurred. The data points for rats fell along straight lines with slopes of 1.16 (first exposure to FI) and 1.32 (second exposure). Thus, in the case of rats, as the value of the schedule was increased, the peak of the response curve occurred later in the interval. The data for pigeons, on the other hand, had fractional slopes of 0.95 (first exposure) and 0.96 (second exposure), indicating that the peak of the pigeons' response curve

Table 1

Fixed-interval values (seconds) and parameter values for normal curve, for data from first, (i), and second, (ii), exposure to the fixed-interval schedules.

Schedule Parameter (sec)	Rats (i)			Pigeons (i)			Rats (ii)			Pigeons (ii)		
	H	M	S	H	M	S	H	M	S	H	M	S
30	37.1	0.90	0.22	85.44	0.86	0.36	78.9	1.17	0.34	99.4	0.88	0.37
60	73.6	0.98	0.47	91.52	0.92	0.45	248.2	1.45	0.58	76.3	0.88	0.42
120	88.4	1.13	0.49	43.06	0.80	0.43	55.2	1.84	0.83	45.3	0.83	0.43

The normal curve is given by the equation:

$$R = H e - \left(\frac{t - M}{S} \right)^2$$

where R is the response rate (responses per minute), t is time expressed as a proportion of the interval, M is the midpoint of the curve, S is proportional to the standard deviation, and H is the height of the curve at $t = M$ (cf. Killeen, 1975).

occurred earlier in the interval on the longer FI values.

Killeen (1975) suggested that M may be taken as an indicator of psychophysical judgement of the duration of the interval and has found that the data from his own study with pigeons (one data point) and from that of Catania and Reynolds (1968) fell along a straight line with a slope of 0.8. On this basis, Killeen proposed that the psychophysical scale of duration for pigeons was a power function with an exponent of 0.8. Previously Catania (1970), on the basis of several studies concerned with the reinforcement of latencies

or IRTs, showed that the temporal spacing of responses could be related, by power functions, to the interval required for reinforcement, and that in rats and pigeons these functions had exponents of slightly less than one. That is, the temporal spacing of responses indicated an overestimation of the schedule value when that value was short and an underestimation when it was long.

Thus, if M is taken as an indicator of a temporal judgement of the interval, both Killeen's analysis of pigeon data and the present results from pigeons are consistent with the existing literature on psychophysical func-

Fig. 7. Rate of responding by rats and pigeons in successive tenths of the interval, in the last four sessions of first exposure to the FI schedules. Data points are averages (geometric means) across animals in each group, for the first nine-tenths of each interval.

Fig. 8. The relation between interfood intervals (T) and midpoint of the normal curve (M). The data are averages across animals in each group, taken from the first (filled circles) and second (filled squares) exposure to the FI schedules.

tions in animals (Catania, 1970; DeCasper and Zeiler, 1974; Platt, Kuch, and Bitgood, 1973). However, the major difficulty for such an account is that the data from rats in the present study cannot be described by a fractional slope. On the contrary, for rats, M increased rather than decreased with the value of the FI schedule. A similar relationship is also to be found in the data of Dukich and Lee (1973), who used rats as subjects. These contrasting functions for rats and pigeons and their relationship to the psychophysics literature are further discussed below.

Figure 8 also shows that although in pigeons there was little difference in midpoint values between first and second exposure to the FI schedules, for rats, the midpoint values were higher on return to the FI schedules. The reasons for this change in the rats' performance are not clear, but it is interesting that although the other measures failed to reflect any change in performance, the midpoints of the curves showed orderly and marked increases.

GENERAL DISCUSSION

Species Differences

These analyses have revealed three major differences in the schedule performance of rats and pigeons: (i) in many cases, rats do

not respond for response-independent reinforcement but pigeons respond at high rates, (ii) rats' responding on FI schedules shows sensitivity to temporal factors not shown by pigeons, and (iii) in rats, the peak of responding on FI schedules bears a different relationship to the FI parameter than it does in pigeons.

One possible explanation of these results is that these differences reflect a basic difference in the particular responses chosen for study; that is, unlike the lever pressing of rats, the pigeons' key peck is itself a consummatory response, or closely resembles the consummatory response (*cf.* Jenkins and Moore, 1973; Wolin, 1968). There is evidence that in a number of different species, stimuli that signal food presentation may come to elicit consummatory behavior (Breland and Breland, 1961), and that temporal factors may enter into the control of food-induced pecking in pigeons (Staddon and Simmelhag, 1971). Thus, whenever reinforcement is presented regularly in time, as it is on both FI and FT schedules, key pecking may be elicited as the time for food presentation approaches. And given that pecking has been trained to be directed at the response key on the FI schedule, it continues to be directed there on the FT schedule. If, on the other hand, regular presentation of food induces any response in

the rat, it will most likely be waiting near or going to the food tray (*cf.* Staddon, 1977) which would, of course, interfere with lever pressing. Consequently, behavior induced by food presentation may enhance key pecking but retard lever pressing on FT schedules.

This hypothesis casts doubt on Killeen's (1975) suggestion that the peak of the normal curve fitted to local rate data represents an animal's ability to estimate the duration of the interval. Rather than being a simple measure of temporal discrimination, the midpoint of the normal curve may be the result of an interaction between reinforced and food-induced responding. Since the response induced by food is compatible with the reinforced response in the case of pigeons, but is incompatible with the reinforced response of rats, it is not surprising that there should be contrasting midpoint functions for key pecking in pigeons and lever pressing in rats, as was found to be the case in the present study.

The differences in the postreinforcement pause/running rate and in the postreinforcement pause/IRT relationships for rats and pigeons may be similarly related to the presence of food-elicited pecking in pigeons since, as some investigators have suggested, elicited pecking is not as sensitive to temporal variables as is pecking that is controlled by reinforcement (Schwartz and Williams, 1972).

The performance of rats and pigeons differs also on differential-reinforcement-of-low-rate (DRL) schedules, where considerably higher proportions of rats' responses are reinforced than those of pigeons (Richardson and Loughhead, 1972; Staddon, 1965). There is evidence, however, that while pigeons can readily discriminate time intervals, they are unable to withhold pecking until a time when reinforcement is available (Reynolds, 1966). Moreover, Hemmes (1975) argued that pigeons' performance on a DRL schedule becomes more like that of rats when the response of stepping on a treadle, instead of key pecking is studied (but see also Richardson and Clark, 1976). This evidence supports the hypothesis that the differences in the performance of rats and pigeons on time-related schedules reflect special characteristics of the key-pecking response. As well as being consistent with much of the existing literature, this hypothesis has the additional merit of

being easily testable; it is only necessary to study different types of response in rats and pigeons.

There are probably many implications of this account for explanations of behavior in general. Notably, the present findings suggest that the differences between rats' and pigeons' time-related behavior do not represent "constraints" on learning and do not necessarily limit the generality of the principles of learning (*cf.* Bolles, 1972; Hinde and Stevenson-Hinde, 1973; Seligman, 1970). Rather, it is becoming clear that the presentation of a reinforcer is a complex event that may have any or all of several effects; it will, of course, in the first instance, reinforce behavior; it may function as a discriminative stimulus, and/or an inhibitory stimulus (Lowe *et al.*, 1974; Reid, 1957; Staddon, 1972); and, as the present data indicate, the reinforcer may have response-eliciting effects. None of these properties of reinforcing stimuli indicates a failure of the principles of learning; rather, the present study suggests that it is only through a full understanding of such principles, in all their complexity, that species differences in behavior may be adequately comprehended.

Moreover, these findings point to the dangers of an emphasis on the formal characteristics of behavior at the expense of controlling relations; what Skinner (1969) termed the "formalistic fallacy". The fallacy in this case is to assume that, because on a given schedule cumulative records or other measures of behavior look the same for animals of different species, the determinants of these behaviors are also the same. Another form of this fallacy, which is even more frequently encountered, is the assumption that because there are differences in the recorded behavior there are no similarities in determining factors.

Implications for Analyses of Fixed-Interval Performance

Recently, there have been suggestions that performance on FI schedules can be considered to consist of two components: (i) time from reinforcement to the first response, and (ii) time from the first response in an interval until next reinforcement. Schneider (1969) and Shull, Guilkey, and Witty (1972) have proposed that the duration of the postrein-

forcement pause and the response rate in the running time are relatively independent, affected by different factors. The results of some studies in which the response/reinforcement contingency or the response unit were manipulated have supported this proposition. Shull (1970, 1971) found that on three schedules, FI, FT, and conjunctive fixed time:fixed ratio 1, the duration of the postreinforcement pause varies as a function of the minimum interreinforcement interval, but it is unaffected by changes in the response/reinforcement contingencies. Similarly, when the running rate is manipulated by introducing "pacing" procedures, i.e., a minimum IRT is required after the elapse of the fixed interval for reinforcement to occur, the postreinforcement pause remains relatively constant but the running rate fluctuates according to the minimum IRT contingency (Farmer and Schoenfeld, 1964; Elsmore, 1971). Similar results are also found when the response unit is changed from one response to 10 or even to 20 responses (Shull *et al.*, 1972) or when responding is interrupted by blackouts (Neuringer and Schneider, 1968; Schneider and Neuringer, 1972). On the basis of these results, advocates of the two-component analysis have concluded that factors associated with the temporal parameters of the schedule determine the subject's time allocation between pausing and responding, while the rate and topography of responding in the terminal state is determined by the responding that prevails at the time of reinforcement. These two sets of determining factors have been considered to be relatively independent.

The present findings show, at least in the case of rats, that the rate of response in the running time is a direct function of the duration of the preceding postreinforcement pause. Temporal factors would appear to be strong determinants of performance throughout the fixed interval, regardless of "component". Moreover, it appears that the duration of the postreinforcement pause is not determined solely by the interreinforcement interval, but is related to the response/reinforcer contingency. On the one FI schedule that produced a substantial decline in pigeons' running rate, the durations of postreinforcement pauses increased markedly for all four subjects. Thus, these data show that on FI schedules, the postreinforcement pause and response rate in the

running time may be related and not independently determined.

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