

The Comparative Psychology of Fixed-Interval Responding: Some Quantitative Analyses

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Data on variation in the average relative frequency of responding with elapsed time since reinforcement during various fixed-interval schedules were available from cats, rats, woodmice, pigeons, turtle doves, a fish species *Tilapia*, and freshwater turtles. These data were analyzed in a uniform manner by fitting Gaussian curves to the response frequency versus time functions, with the curve peak forced to be at the fixed-interval value. This analysis yielded a curve coefficient of variation (curve standard deviation/peak location), a measure of the precision of within-interval temporal control. Overall, Gaussian curves fitted data well, and two general trends could be noted. First, curve coefficient of variation tended to increase with increases in the fixed-interval value (although for most species used a range of interval values could be noted over which the coefficient of variation remained approximately constant). Second, different species differed markedly with respect to the absolute value of coefficient of variation obtained, by implication the quality of temporal control manifested. Lowest values (i.e., best temporal control) were obtained in data from cats, rats, and mice (as well as data from monkeys taken from another study). Pigeons produced higher values, then fish, then turtle doves (whose temporal control was markedly worse than that exhibited by pigeons), and finally turtles. A simple model deriving responding during fixed intervals from a mixture of timing and nontiming processes predicted that curve coefficient of variation would increase with interval value, even if the sensitivity of an underlying timing mechanism were constant. The model thus reconciled an underlying scalar timing process with obtained behavior, which at first sight violated scalar timing. The model further suggested that different species probably did differ in their underlying timing capacity, as the amount of response generation resulting from nontiming processes would need to be implausibly large to reconcile all the obtained coefficients of variation with an underlying timing process of uniform sensitivity. © 1991 Academic Press, Inc.

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For more than 50 years, since their invention by Skinner (1938), fixed-interval (FI) schedules of reinforcement have been an important part of the experimental repertoire of behavioral psychologists. On a standard FI schedule the essential aspect of the reinforcement contingency involves the *time* since a previous reinforcer was delivered. For example, in a typical experimental session, the first response in the session will be reinforced, and this reinforcer delivery starts a clock. The clock runs for a fixed length of time, t s, which is the FI schedule parameter, and while the clock is running responses have no scheduled consequences. When the clock times out, the *next* response emitted by the subject is reinforced. This reinforcer delivery restarts the clock, which runs for another t s, and so on.

The pattern of behavior emitted on FI schedules of food reinforcement by common laboratory animals after a number of sessions of training exhibits clear temporal regularities (Dews, 1970). Food delivery generally initiates a pause in responding (the postreinforcement pause), after which responding either gradually accelerates up to the next reinforcer delivery (producing the classic FI "scallop"; see Dews, 1978, and Lowe and Harzem, 1977, for some clear examples from rhesus monkeys and rats), or occurs at a high, constant rate up to the next reinforcer delivery (a "break and run" pattern; e.g., Schneider, 1969).

Quantitative analyses of the pausing behavior occurring under FI schedules reveal that it conforms to a number of psychophysical principles. For example, the length of the postreinforcement pause grows as a power function of the FI value in both rats and pigeons (Lowe, Harzem, & Spencer, 1979; Wearden, 1985). Furthermore, postreinforcement pauses produced under FI conform to the Generalized Weber law, in that their standard deviation is a linear function of the mean (Lowe & Wearden, 1981). Conformity of behavior to both the power law and Weber's law is a common result on temporal differentiation schedules, in which some time requirement on properties of responding, such as response spacing, is imposed as a condition for reinforcement (see Platt, 1979), and simultaneous conformity to the two laws of behavior can be reconciled by some multiprocess theories of animal timing (such as Wearden, 1985). Such regularities in performance clearly suggest that the FI schedule might be useful in investigating underlying timing processes in animals, and a variant of the FI schedule (called the *peak procedure*, Roberts, 1981, 1982) has indeed been utilized to test the well-known *scalar timing* theory (Gibbon, 1977).

The peak procedure involves a discrete-trial technique in which most trials of the experimental session are programmed similarly to a standard FI, except that the start of the trial is signaled by a light or a tone, rather than food delivery. Following this, subjects are reinforced for the first lever press occurring more than t s after the start of the trial. Another

type of trial is randomly interspersed with the FI trials; this type is much longer than the standard, t , and terminates independent of responding. For example, in Roberts (1981, Experiment 1), the standard FI was either 20 or 40 s, so food was delivered for the first response after these times on 80% of trials, with the remaining 20% of trials terminating after 80 s plus a random time, independent of behavior. Measurement of responding during these longer trials revealed that response rates increased systematically throughout the interval up to the normal time of food delivery (20 or 40 s, in this case), then declined systematically thereafter. Roberts (1981) fitted curves to the response rate versus time functions and found two theoretically important results. The first, which was most strongly supported by the data, was that the peak of the response rate function coincided closely with the standard FI value, as this was varied. The second, for which evidence was less strong, was that the coefficient of variation of the fitted curve (the standard deviation of the curve divided by the peak location) remained constant as the standard FI varied.

Both of the obtained results (near-coincidence of peak location and FI value, and constant coefficient of variation) are predictions of scalar timing theory. A full discussion of this theory can be obtained elsewhere (e.g., Gibbon, 1977; Gibbon, Church, & Meck, 1984), but for present purposes it is sufficient to note that, according to scalar timing theory, (i) mean estimates of some clock time, t , vary linearly (and in most cases accurately) with t , and (ii) Weber's law is obeyed in the sense that the coefficient of variation of the timing mechanism (a type of Weber fraction) remains constant as clock time, t , is varied.

On a standard FI schedule only the left-hand half of Roberts' response rate versus time functions can be observed, as the first response occurring more than t s after the previous reinforcer restarts the interval. Nevertheless, responding during standard FI schedules can still be used to examine the second prediction of scalar timing theory, namely that the coefficient of variation of an underlying timing mechanism remains constant as the interval is varied, as will be seen later.

The present article has two slightly different, but related, aims and is unusual in that performance under FI schedules is examined explicitly in a cross-species context. The first aim is to investigate whether the scalar timing prediction of constant coefficient of variation is violated within any single species as the FI value is varied and, if it is violated, to attempt to explain why. The second aim is to compare the performance of *different* species on FI to attempt to ascertain if different species differ systematically in the type of temporal regulation that they exhibit on this schedule.

The comparative study of behavior under FI schedules is not new. Sometimes, however, only "standard" laboratory species such as rats and pigeons have been compared (e.g., Lowe & Harzem, 1977). In other

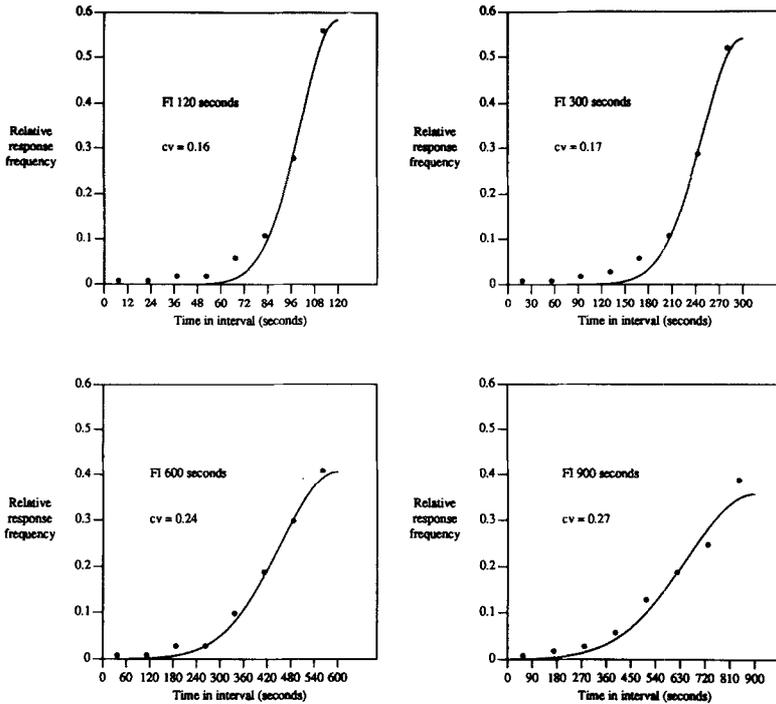


FIG. 1. Relative response frequency versus time in FI in data from cats. Each panel shows the data points (filled circles), the best-fitting Gaussian curve (solid line), FI value in seconds, and curve coefficient of variation (cv).

cases, data from a much wider variety of species have been reviewed (e.g., Richelle & Lejeune, 1980, 1984), but the measures of behavior available (such as indices of curvature, Fry, Kelleher, & Cook, 1960) are difficult to relate to contemporary quantitative analysis and theory. A vast literature on FI performance of different species has been amassed over the years (see Richelle & Lejeune, 1980, 1984, for reviews), but data obtained from many unusual species are unsuitable for quantitative analyses (e.g., cumulative records of FI performance in honey bees, Grossman, 1973). In the present article, we will make no systematic attempt to review this vast corpus, but instead concentrate on a range of species for which we have quantitative data which can be analyzed in a uniform manner. Even concentrating on a subset of available work, our range of species is large relative to that used by other authors, ranging from cats and mice to fish and freshwater turtles.

Analytical Procedure

The analytical technique we use in the present work can be illustrated by reference to the data shown in Fig. 1. The subjects were adult cats,

responding with lever-presses reinforced with milk under FI values of 120, 300, 600, and 900 s (for the original experimental report, including measures of behavior such as cumulative records, see Lejeune, 1971). Raw data were available on the relative frequency of responses during 8 successive bins making up the interval length. The data come from the last experimental session (which lasted between 60 and 135 min, depending on FI value), where between 20 and 67 sessions of exposure had been given at the various schedule values, and data are averaged over 3 or 5 cats, depending on condition. A Gaussian curve was fitted to the relative frequency distributions by the nonlinear regression subprogram of the BMDP statistical package. The independent variable (time in interval) was the time represented by the midpoint of the appropriate bin, e.g., 7.5 and 22.5 s for the first two bins of FI 120 s, the dependent variable the relative frequency of responding. The peak of the Gaussian curve was forced to be at the interval value (e.g., 120 s for FI 120), unlike the curve-fits of Roberts (1981) where the peak was allowed to vary. This was done for several reasons: first, inspection of the data suggested that peak response frequency almost invariably occurred in the last bin (as in all the panels of Fig. 1) so the peak response frequency was probably not to be found at any time lower than the FI value; second, since no postreinforcement times higher than the FI parameter are available, any curve-fit which suggests that response rate would peak at a higher value is impossible to evaluate; third, peak procedure analyses such as Roberts (1981) suggest that the response rate under FI-like schedules generally does peak at approximately the FI value; finally, forcing the peak of the curve to be at the FI value rarely seemed to do violence to the data, as the proportion of variance accounted for by the fitted curve was almost always high, often 95% or more.

Given that the peak of the Gaussian curve is forced at the FI value, the curve-fit yields two free parameters. One is the standard deviation of the curve, which for Gaussian functions is located at the point at which the slope of the curve changes from positive to negative (i.e., its point of inflection, see Meyer, 1970, p. 183). The other (which is not meaningful when relative frequency data are used) is a multiplier converting probability values into frequencies or rates. The standard deviation obtained from the curve fit was divided by the FI value to yield a coefficient of variation, and statistics provided by the nonlinear regression were used to calculate the proportion of variance accounted for by the fitted curve. Unless otherwise indicated, all data analyses performed in this article used the method described above.

Consider now the actual results in Fig. 1. As well as showing data points and the fitted curve, each panel also gives the coefficient of variation of the curve. Inspection of Fig. 1 suggests two obvious conclusions; first, that the Gaussian curve generally fitted data well (in fact, minimum proportion of variance accounted for by the curves shown in Fig. 1 was 97%);

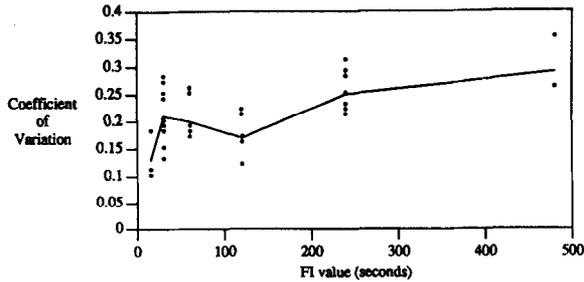


FIG. 2. Coefficients of variation of Gaussian curves fitted to response frequency versus time functions from rats at FI values from 15 to 480 s. Data points (some of which are superimposed) are shown as filled circles. A solid line connects the mean coefficient of variation at each FI value used.

second, the coefficient of variation of the fitted curve increased systematically (from 0.16 to 0.27) as the FI value increased. Both the data points and the quantitative analysis indicate, however, that behavior was temporally well-regulated in cats even at the longest FI value.

Data in the form of those shown in Fig. 1 thus address the first question posed above and suggest that, within the cat species at least, coefficient of variation of relative response frequency versus time functions increases systematically, although not very markedly, as FI values increase from 120 to 900 s. To address the second question posed, we must turn to some cross-species comparisons.

Cross-Species Comparisons

We next consider data from two rodent species, rats and woodmice (*Apodemus sylvaticus*). The rats were hooded rats, obtained from laboratory animal suppliers; the woodmice were trapped in the wild in Liège. Both species pressed levers under FI schedules of food; schedule values ranged from FI 15 to FI 480 s with rats, and from FI 30 to FI 240 s with mice.

Figure 2 shows coefficients of variation of fitted Gaussian curves plotted against FI values for individual rat subjects, some of whom contributed more than 1 data point in replications or at different schedule values. FI schedules were in force for a minimum of 18 sessions, but usually for a longer period, and data were taken from the last three or five sessions. The line in Fig. 2 connects the mean of the coefficients of variation shown. Raw data came from Whitaker (1979) and an unpublished experiment by C. F. Lowe (kindly made available to the present authors). Curves were fitted in the manner described above, except that a specially written curve-fitting program was used rather than BMDP. Proportions of variance accounted for by the fitted curves were all 85% or more, and most were 90% or more.

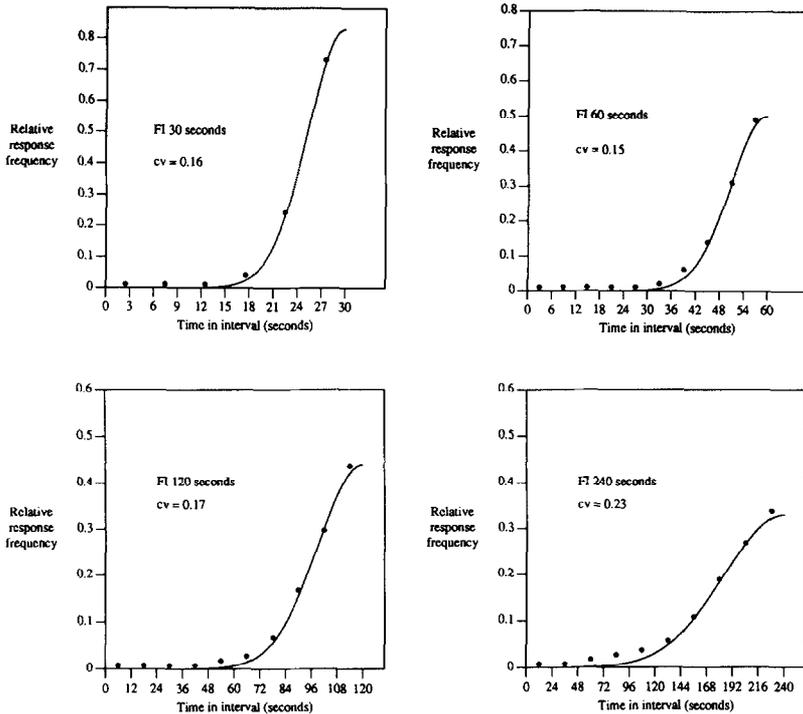


FIG. 3. Relative response frequency versus time in FI in data from woodmice. Each panel shows data points (filled circles), the best-fitting Gaussian curve (solid line), FI value in seconds, and curve coefficient of variation.

Inspection of Fig. 2 suggests, as in the case of cats, that coefficients of variation of the fitted curves tended to increase as the FI value increased, although they showed no systematic change over schedule values ranging from FI 15 to FI 120 s. Figure 2 also indicates a degree of intersubject variability in coefficient of variation value within this general trend.

Figure 3 shows Gaussian curves fitted to relative response frequencies versus time functions from an experiment with woodmice. Data are averaged over 3 mice, come from the last 3 sessions of schedule exposure (which lasted from 10 to 41 sessions), and FI parameter ranged over values of 30, 45, 60, 120, 180, and 240 s. For clarity, only results from FI values of 30, 60, 120, and 240s are included in Fig. 3. Inspection of Fig. 3 suggests that (i) the Gaussian curves fitted data well (in fact, all accounted for 99% of variance) and that (ii) coefficient of variation, once again, tended to increase with increasing FI, although it was roughly stable from FI 30 to FI 120 s. Data from the schedule conditions not shown in Fig. 3 were almost identical to those presented: coefficients of variation were 0.14 at FI 45 and 0.19 at FI 180 s; all curves accounted for 99% of data variance.

Comparison of the results from all three mammalian species included here (cats, mice, and rats) reveals several striking qualitative and quantitative similarities. In all cases, Gaussian curves fitted data very well, and in all cases the coefficients of variation of the curves increased with FI value, although they all tended to remain stable over a wide range of FI values (120 to 300 s in cats, 15 to 120 s in rats, 30 to 120 s in mice). The actual values of coefficients of variation obtained were also very similar in the three species. Although there is a suggestion in the data that coefficients of variation from rats were the highest, the different FI values used and the fact that coefficient of variation values in the three species tend to overlap, preclude firm conclusions. Overall, in general, at the lower FI values used, coefficients were generally less than 0.2, whereas all three species produced coefficients between 0.2 and 0.3 at the longest FI value employed. We turn next to data from the study by Lejeune and Richelle (1982), which conducted an explicit comparison of FI performance in rats and two bird species.

From Rats to Birds

Lejeune and Richelle (1982) compared Wistar strain rats, homing pigeons, and domestic turtle doves (*Streptopelia risoria*), on FI schedules ranging from FI 120 to FI 600 s. Care was taken to equate the procedures used for the three species so far as was practicable. Rats lever-pressed for 45-mg food pellets, and both bird species key-pecked for 3 s access to grain. Standard experimental chambers were used. Four subjects of each type received increasing FI schedule values after an initial session of continuous reinforcement training, with the FI value incrementing by 10 s each session. When FI 120 s was reached, this schedule was maintained for 40 sessions, followed by 30 sessions of FI 240, 30 of FI 360, 40 of FI 480, and 30 of FI 600 s. Session duration lasted for 15 reinforced intervals up to FI 360, then for 12 intervals at the two longer values. Cumulative records and some other measures of behavior may be obtained from the original report (Lejeune & Richelle, 1982). For present purposes, raw data in the form of responses in each of four bins making up the FI value were subjected to a curve-fitting analysis identical to that described above. Only four response bins were available from this study, as data were not collected by computer. This means that comparisons with some of the other data sets used in the present article may not be exact, but in view of the careful procedural comparison of this study, as well as unusual features such as the long FI values employed and data from turtle doves, we decided to include it. Data at each interval value were aggregated across the last three sessions of schedule exposure and all three subjects. Figure 4 shows the resulting coefficients of variation, plotted against the FI value.

Inspection of Fig. 4 indicates clear species differences in the pattern of

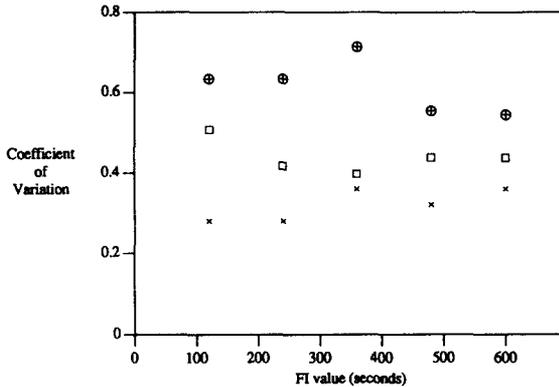


FIG. 4. Coefficients of variation of Gaussian curves fitted to data from Lejeune and Richelle (1982), plotted against schedule value. Crosses show data from rats, squares data from pigeons, circles with cross data from turtle doves.

temporal control exhibited by rats, pigeons, and doves. Lowest coefficients of variation were obtained from rats, with the values derived from the shorter FI values used being similar in absolute value to those shown in Fig. 2. As in Fig. 1, 2, and 3, there was a clear indication that coefficient of variation increased with FI value, although the increase was not large.

Pigeons produced larger coefficients of variation than rats, and these did not increase with the FI; instead, they remained stable (at about 0.44) at values of FI 240 s or more. Lastly, the turtle doves produced the highest coefficients of variation of all, which tended to *decline* with increasing FI, at least in the sense that the two lowest values were obtained at FI 480 and FI 600 s. Even then, however, the coefficients of variation produced by the turtle doves remained higher than the highest values obtained from rats and pigeons.

The principal messages from these data appear to be that (i) temporal regulation of responding under FI in pigeons and turtle doves is poorer than in rats (and in the cats and mice discussed above), and (ii) even closely related bird species such as pigeons and doves can differ substantially in the precision of their temporal regulation, even when many procedural variables (such as reinforcer magnitude, apparatus, and number of training sessions) are perfectly equated. The original report by Lejeune and Richelle (1982) also noted a number of other differences between the species used, principally in terms of the index of curvature (Fry *et al.*, 1960) which mirrored the results shown in our Fig. 4 (i.e., rats had the highest curvature values, pigeons next highest, and doves the smallest), and the appearance of cumulative records. Here, rats and pigeons produced "typical" scalloped or break-and-run patterns, whereas responses produced by the doves tended to be more evenly distributed in the interval,

with the lack of a characteristic lengthy postreinforcement pause being particularly notable (see Lejeune & Richelle, 1982, Fig. 2, for an example).

The careful comparison of rats and birds conducted by Lejeune and Richelle (1982) clearly indicates some degree of degradation of temporal control within intervals as we move from a mammalian to a nonmammalian species. We next consider FI performance of two "lower" nonmammalian species, fish and terrapins.

FI Performance in Fish and Turtles

The fish species used was Tilapia (*Sarotherodon niloticus*), an African cichlid. Subjects responded by a head push on an immersed manipulandum (a translucent plastic disk on a rod) which was illuminated from behind with green light. Reinforcers for these vegetarian subjects were 45-mg Noyes rat pellets dispensed into the aquarium via a plastic tube. All subjects were male. They were successively exposed to FI schedules (2 to 20 s), variable-interval schedules (20 to 60 s), and again to FI (60, 90, and 120 s). Data from the second exposure to FI schedules are used here, with FI 60 s in force for 23 sessions, and FI 120 s for 29 sessions. Data from FI 90 s were not available for analysis. All sessions lasted until 20 reinforcers had been delivered or for 20 min (FI 60 s) or 45 min (FI 120 s). Curvature indices (Fry *et al.*, 1960) and postreinforcement pause values are available in the original report (Grailet, 1983). These indicate that the fish did not improve temporal regulation with increased training. For example, considering data from the first and last five sessions of schedule exposure during the second series of FI schedules mean pause values in seconds (first 5, last 5) were: FI 60 s (25.2, 25.5), FI 120 s (32.5, 32.7). Curvature indices likewise showed little change with training, e.g., FI 60 s (0.343, 0.338), FI 120 s (0.298, 0.301). Data used in the current article were averaged across 6 subjects and come from the last 20 sessions at each schedule exposure. Each FI interval was divided into 10 equal-length bins; relative response frequencies in these bins were used as the dependent variable in the curve-fitting analysis, as described above.

Figure 5 shows relative response frequencies and fitted curves for FI 60 and FI 120 s, as well as curve coefficients of variation. The Gaussian curves fitted data well (97 and 99% of variance accounted for at FI 60 and 120 s, respectively), and coefficient of variation increased slightly as the FI value increased (from 0.46 to 0.50).

The high coefficients of variation obtained in data from Tilapia indicate poor temporal regulation in these subjects. However, inspection of the response rates emitted during different parts of the FI indicated that all individual subjects responded more at the end of the interval than at the beginning, thus exhibiting at least the rudiments of temporal control. The general question of whether Tilapia exhibited any marked degree of true

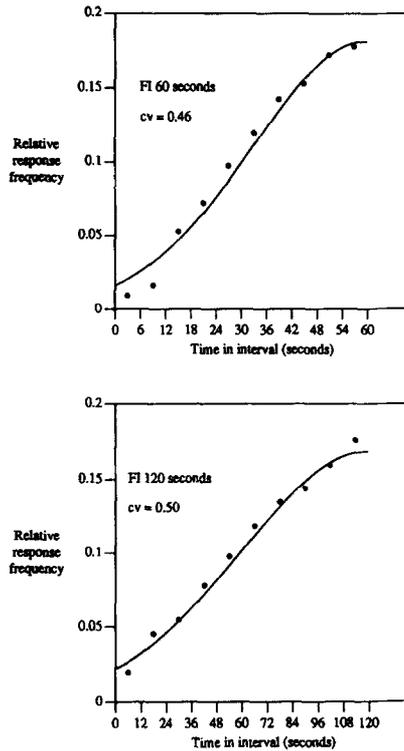


FIG. 5. Relative response frequency versus time in FI in data from a fish species *Tilapia*. Each panel shows data points (filled circles), the best-fitting Gaussian curve (solid line), FI value in seconds, and curve coefficient of variation.

schedule sensitivity, such as changes in rate or patterning when the reinforcement schedule was changed, was investigated by Grailet (1983), who trained *Tilapia* on a fixed-ratio schedule and a variable-interval schedule with the same average interfood interval, as well as the FI schedules discussed above. Some subjects showed evidence of changes in rate and patterning when the schedule type was changed but, overall, the study did not provide conclusive evidence of conventional schedule sensitivity in these subjects.

The other nonmammalian species used was the freshwater turtle (*Pseudemys scripta elegans*). For the original experimental report see Laurent (1983). The response manipulandum was a horizontal red plastic cylinder attached to a rod, and a head push on this cylinder activated a microswitch. Preliminary experimentation had established that this species was attracted by the color red. The reinforcer was small pieces of meat in the form of cat food, as this species is carnivorous, dispensed by a universal feeder.

Subjects were exposed to an extensive period of continuous reinforcement training, during which the size of the red cylinder was reduced from 6 to 3.5 cm. The turtles first received four sessions of FI 5 s, then two of FI 10 s, then three of FI 15 s. Finally FI values of 30, 60, and 90 s were used, and the data presented in this article come from these conditions. Schedules were in force from 14 to 30 sessions, for different subjects, where each session lasted until 25 reinforcers had been delivered. Data are averaged over the last five sessions and all five subjects. As was the case with *Tilapia*, comparison between pause duration and curvature indices averaged over the first and last five sessions at each FI value did not reveal significant changes in performance (Laurent, 1983). Furthermore, average curvature indices remained under 0.1 at all schedule values, a value much lower than obtained from fish (see above).

Figure 6 shows response rate during 10 bins at each interval value, and the fitted Gaussian curve as well as curve coefficient of variation. The curve-fitting procedure was as in the standard case described above, with the exception that the response rate in the first bin was not used for the fit (i.e., only bins 2 to 10 were used).

Inspection of Fig. 6 suggests that, once again, the Gaussian curves fitted data well (the proportions of variance accounted for were 94% at FI 30 s, 91% at FI 60 s, and 86% at FI 90 s), when data from the first bin are ignored. The obvious interpretation of the response rate in this first bin is "overshoot," that is, some time is required for the reinforcer to be dispensed, and the subject continues to respond until the reinforcer is delivered. Coefficients of variation typically increased as the FI value increased, from 0.60 to 0.79.

Comparison of data from fish and turtles suggests that, as in mammals, coefficients of variation of fitted curves increased with the FI value. The most striking difference between the mammals and nonmammals compared in this article is that the quality of temporal regulation was much worse in fish, turtles, pigeons, and turtle doves than in cats, rats, and mice. The values of coefficients of variation obtained strongly support this assertion, as there is no overlap between the smallest coefficient of variation from the nonmammals (just over 0.4, from the pigeons shown in Fig. 4), and the largest obtained from mammals (0.36, Lejeune and Richelle's rats at FI 360 and 600 s). Another indicator of poor temporal control in the turtles came from inspection of the response frequency versus time functions produced by individual subjects. Unlike cats, rats, mice, and *Tilapia*, all of whom produced clear evidence of temporal control within intervals of FI when individual subject data were examined, turtles produced clear evidence of temporal regulation only when data were averaged: Some individual subjects exhibited little or no evidence of temporal regulation of responding.

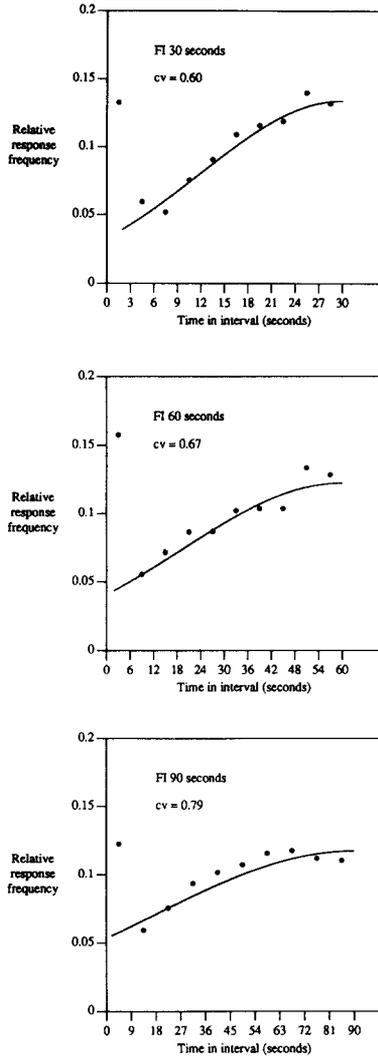


FIG. 6. Relative response frequency versus time in FI in data from freshwater turtles. Each panel shows data points (filled circles), the best-fitting Gaussian curve (solid line [Note that in this case the data point in the first frequency bin was not used for the fit]), the FI value in seconds, and the curve coefficient of variation.

Some General Trends

As well as processing the data sets shown in Fig. 1 to 6, which were analyzed from raw numerical values, we also fitted Gaussian curves to data from two other studies, which gave results in a suitable form in their published versions. Data from pigeons on FI values of 30, 60, and 120 s

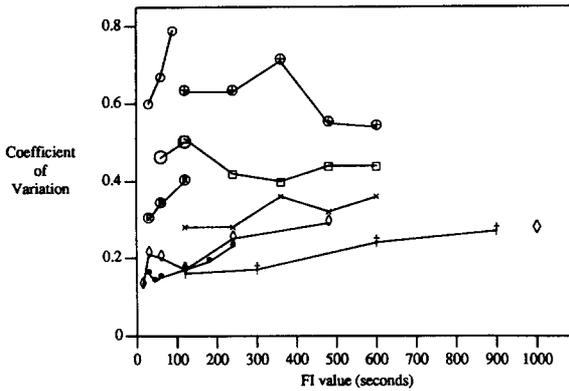


FIG. 7. Coefficient of variation of fitted Gaussian curves plotted against the FI value. The figure summarizes material in Fig. 1 to 6, and includes some other points. Key: small filled circles, woodmice; small open circles, freshwater turtles; small diamonds, rats from Whitaker (1979) and Lowe (unpublished); larger diamond, rhesus monkeys from Dews (1978); x, rats from Lejeune and Richelle (1982); †, cats; larger circles, Tilapia; ⊗, pigeons from Lowe and Harzem (1977); squares, pigeons from Lejeune and Richelle (1982); circles including crosses, turtle doves from Lejeune and Richelle (1982).

were taken from Lowe and Harzem (1977, Fig. 7, p. 197). Lowe and Harzem fitted curves to response rates during nine bins, but as their curve-fitting procedure was somewhat different from ours, we measured response rates from their Fig. 7 and reanalyzed them. Gaussian curves with peaks located at the FI value accounted for 99% of variance in all cases. We also measured averaged data from Dews (1978, Fig. 3). Here, two rhesus monkeys responded on a multiple FI 1000 fixed ratio 50 schedule, which had been in force for more than 300 sessions, and data were taken from the FI component. Only a single FI value (1000 s) was available. Once again, Gaussian curves accounted for 99% of data variance. The coefficients of variation from pigeons and the two monkeys (both of whom produced the same value), as well as those from the other species whose data are shown in Fig. 1 to 6 are plotted in Fig. 7.

Consider first coefficients of variation from Lowe and Harzem's (1977) pigeons and Dews' (1978) monkeys. Values from pigeons increased from 0.3 to 0.4 as FI value increased; the value from both the monkeys was 0.27 at FI 1000 s. Figure 7 also clearly shows the within- and between-species trends in coefficients of variation. In most species for which a range of FI values was available, coefficient of variation increased with increasing FI (although it was often stable, or unsystematically variable, over a reasonably wide range of FI values). Not only was this general trend obvious on inspection, but the tendency for coefficient of variation to increase with FI value was statistically reliable in most data sets. Linear regression of coefficient of variation against FI value was applied to all

cases in which 3 or more data points were available. Significant positive slopes ($p < 0.05$) were obtained in data from cats, woodmice, Lowe and Whitaker's rats, Lejeune and Richelle's rats, and Lowe and Harzem's pigeons. A nonsignificant positive slope was exhibited by data from turtles, and results from Tilapia were not analyzed, as only 2 points were available. In both of these data sets, however, there was a monotonic increase in coefficient of variation with FI value. Neither the pigeons nor doves from Lejeune and Richelle (1982) showed significant trends in coefficient of variation with changes in FI.

Between species there were marked differences in the coefficient of variation value obtained, and by implication in the quality of temporal regulation on FI. "Higher" animals such as cats and monkeys showed good temporal regulation even on very long FI values; rats and mice regulated well at short FI values but were poorer at longer ones; pigeons came intermediate between rodents and fish; turtle doves were markedly poorer than pigeons; and last, turtles produced very large coefficients of variation, as well as other indicators of poor temporal regulation.

Given that most of the studies from which data are presented in this article were not specifically undertaken with a view to determining asymptotic performance at each FI value used, some of the trends noted above might be artifacts deriving from trival methodological variables such as number and duration of sessions. For example, coefficients of variation from Lowe and Harzem's (1977) pigeons were lower than those from the pigeons used by Lejeune and Richelle (1982), but this difference may partly arise from the longer schedule exposure in Lowe and Harzem's study, or the fact that the FI values employed by Lejeune and Richelle were generally longer than those used by Lowe and Harzem. This state of affairs underscores the need for truly comparative experimentation, some guidelines for which might be found within the theoretical framework discussed in the final section of the present article.

Scalar Timing and FI Performance

As noted above, the peak procedure, a sort of modified FI schedule, has often produced data supporting scalar timing theory (e.g., Roberts, 1981). What are the implications of the results presented in the summary in Fig. 7 which are derived from standard FI schedules, for this theory?

If coefficients of variation derived from relative response frequency are taken as *directly* reflecting underlying timing processes (i.e., not as the result of some other process in addition to timing), the data in Fig. 7 present a mixed picture for scalar theory. On the positive side, some data sets (Whitaker and Lowe's rats, our mice, rats, pigeons, and doves from Lejeune & Richelle, 1982) exhibit a range of FI values at which coefficients of variation of fitted Gaussian curves change little or vary unsystematically. On the negative side, all the data from mammals coming from a range

of FI values show a consistent trend for coefficient of variation to increase with FI value. The same trend is found in Lowe and Harzem's (1977) pigeons, the fish species *Tilapia*, and freshwater turtles, even though relatively few data points are available. Only in Lejeune and Richelle's (1982) data from pigeons and doves is there any evidence of a *decline* in curve coefficient of variation with increases in FI value. Overall, therefore, the scalar timing theory prediction of constant coefficient of variation is strictly violated by the data in Fig. 7, although for some species a range of FI values can be found over which it holds.

However, the assumption that coefficients of variation obtained from our curve-fitting procedure are the pure products of timing processes may be implausible. Suppose, rather, that the responding that occurs within FI schedules is the product of two processes, one of which is "pure timing," and the other of which is response generation within the interval which is random with respect to time. Several previous authors (Gibbon, 1971; Wearden, 1985; Zeiler, 1981) have proposed hybrid models of this sort to account for situations in which observed behavior appears to deviate markedly from scalar predictions (such as the fact that the postreinforcement pause under FI varies as a power function of the FI value; e.g., Wearden, 1985). We now develop a simple model along these lines and evaluate its implications for FI *responding*, in particular for the values of coefficients of variation which are obtained when our standard curve-fitting procedures are applied to simulated results.

Our model is a direct derivative of that of Wearden (1985), and embodies essentially the same idea. Consider an FI schedule lasting for 100 arbitrary time-units, at each of which one or more responses can occur. Suppose that one response-generating process is timing-related and is on average represented by a Gaussian growth process, reaching its maximum at the FI value (100 time-units), and growing according to some coefficient of variation, c . This produces a curve standard deviation of c times the FI value, in the first case considered $100c$. The growth process is scaled so that response probability is 1.0 at time-unit 100. Operating alone, the timing process would therefore produce, when responses from a number of intervals were aggregated together, a Gaussian curve with a peak at the FI value and a coefficient of variation, c . However, responses can also be generated by a nontiming process, which has probability p of producing a response at each time-unit within the FI interval, regardless of time since reinforcement. Obviously, this nontiming process, operating alone, would produce a uniform distribution of responses within the fixed-interval period.

The upper panel of Fig. 8 shows some results from a simulation embodying the above ideas. 100 FI intervals were simulated to produce each point shown, the coefficient of variation of the underlying Gaussian growth process remained constant at 0.25, and the probability per unit time of

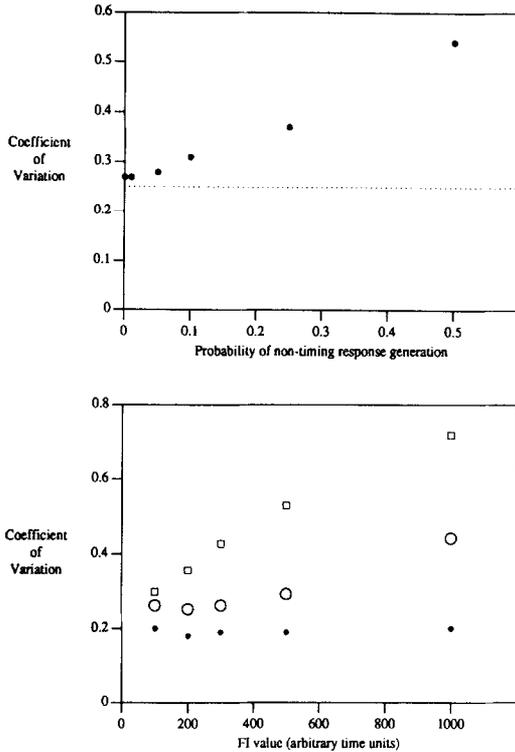


FIG. 8. *Upper panel:* Coefficient of variation of curve fitted to simulated results from a standard FI 100 (filled circles), as a function of probability of nontiming response generation, according to the model discussed in the text. The coefficient of variation of the underlying timing process remained constant at 0.25, as shown by the dotted line. *Lower panel:* Coefficient of variation of curve fitted to simulated data as FI value varied from 100 to 1000 time-units (see text for discussion of model). Points shown come from conditions varying the coefficient of variation of the underlying timing mechanism (first parameter), and probability of nontiming response generation per unit time (second parameter). Conditions shown are 0.15, 0.01 (filled circles), 0.20, 0.05 (open circles), 0.25, 0.10 (squares).

a nontiming response varied from 0 to 0.5. Responses from the 100 simulated intervals were grouped to form relative response frequencies in each of 10 equal-length bins within the interval of 100 time-units. These relative frequencies were subjected to a curve-fitting procedure identical to that used on data in this article, and the upper panel of Fig. 8 shows the resulting changes in obtained coefficient of variation as the probability of a nontiming response per unit time within the interval varies.

The upper panel of Fig. 8 illustrates the intuitively obvious result that adding a larger and larger component of nontiming responses by increasing the probability of this process increases the coefficient of variation of the resulting response frequency versus time function. What is less intuitively

obvious is how much nontiming responding needs to be added to the underlying time-related control of behavior to substantially change the coefficient of variation obtained by curve-fitting. It is clear from the upper panel of Fig. 8 that, for example, a coefficient of variation of less than 0.3 (a typical result from mammals) and the higher values of 0.5 or more (obtained from turtle doves, fish, and turtles) can only be reconciled with the *same* underlying coefficient of variation of the putative timing mechanism if a very large amount of nontiming responding was occurring in turtles, fish, and turtle doves, and very little in mammals. The situation becomes worse if we try to reconcile *all* the coefficients of variation obtained in the data and shown in Fig. 7 with the *same* underlying coefficient of variation, which is essentially equivalent to assuming that *all* the species discussed in the present article have the same underlying timing sensitivity. To do this we would need an underlying coefficient of variation at least as small as that produced by rats at FI 15 s, which would necessitate a very high level of nontiming control of behavior in species such as turtles and turtle doves. Thus, the present model offers a potential method of reconciling any two coefficients of variation obtained from measures of behavior with the same underlying timing process, merely by adding different amounts of nontiming behavior. It may, however, be much more plausible to assume that different species really do differ in timing sensitivity, as well as perhaps differing in the degree to which responses occurring during FI intervals are generated by nontiming sources of control.

The idea that responding during intervals of an FI schedule is derived in part from nontiming sources may also be useful in understanding why, in the data shown in Fig. 7, coefficients of variation of obtained response functions generally tend to increase as FI value increases, and why, conversely, they sometimes remain constant over a range of FI values.

If a nontiming process has a constant probability of generating a response per unit time, then more responses will be generated during longer absolute times. Thus, one might expect that hypothesized nontiming sources of response generation would make a larger absolute contribution to response functions at longer FI values than at shorter ones, and they will also make a larger relative contribution if the overall response rate generated by the timing process decreases as the FI interval grows, as data suggest it does in practice (e.g., Lowe *et al.*, 1979). Since the contribution of nontiming response generation is to increase coefficient of variation of response functions, the obvious prediction is that such coefficients will grow as the FI value grows, even though the sensitivity of the underlying timing process (the coefficient of variation of the Gaussian growth curve) remains constant, and even though the probability of a nontiming response per unit time remains constant. The lower panel of Fig. 8 evaluates this prediction by simulation.

Three conditions are shown which differ both in underlying coefficient of variation of the timing process (varied over values of 0.15, 0.20, and 0.25) and in the probability of a nontiming response per unit time (varied over values of 0.01, 0.05, and 0.10). 100 intervals at FI values of 100, 200, 300, 500, and 1000 time-units were simulated, relative frequencies of responding were calculated, and curves were fitted to these functions, as in the data analyses presented above. The lower panel of Fig. 8 shows resulting coefficients of variation.

An important preliminary point is that, for each of the three sets of simulated data shown in the lower panel of Fig. 8, the simulation parameters do not change as the FI value changes. Any change in resulting coefficient of variation with FI value is thus a result of the change of FI value itself. Inspection of the lower panel of Fig. 8 suggests that a variety of possible changes in data coefficient of variation with increases in FI value might be expected, depending on the probability of nontiming response generation. When this is very low (0.01 per unit time, as in the 0.15, 0.01 condition, filled circles) obtained coefficient of variation remains constant with FI value. Obviously, this occurs because the nontiming process makes a very small contribution to behavior at all FI values. Conversely, when probability of nontiming response generation is much larger (0.1 per unit time, as in the 0.25, 0.1 condition, squares), obtained coefficients of variation will increase systematically with increases in FI value. Last, at an intermediate level of nontiming response generation (0.05 per unit time, as in the 0.20, 0.05 condition, open circles) obtained coefficients of variation will remain constant over a range of lower FI values, then increase at higher ones.

These latter two cases are represented in experimental data by (i) Lowe and Harzem's (1977) pigeons, Tilapia, and freshwater turtles, and (ii) by all the mammals whose data, derived from a range of FI values, are shown in Fig. 7, that is, rats, mice, and cats. Thus, it is clear that an increase in obtained coefficient of variation with FI value may be rendered completely compatible with underlying constant coefficients of variation of timing processes, if it is assumed that a proportion of responses is generated with some constant probability per unit time without respect to elapsed time in the interval.

Our simple model thus offers some potential support for the scalar timing prediction that coefficients of variation of underlying timing processes remain constant as the interval to be timed varied. This assumption, along with some relatively small probability of nontiming response generation, is compatible with most of the results shown in Fig. 7. We may assume, in addition, that different animal species differ both in terms of underlying timing sensitivity and susceptibility to nontiming control of behavior. Animals such as cats who exhibit well-regulated FI responding even on very long FI values must not only have a relatively small un-

derlying coefficient of variation in their timing mechanism, but must also have an absolutely small probability of response generation by nontiming sources of control. If this latter requirement were not fulfilled, coefficients of variation would increase more sharply with increasing FI value than is the case, for example, in data from cats shown in Fig. 7.

In summary, our model offers a way to reconcile coefficients of variation obtained from data in different species with the *same* underlying degree of timing sensitivity, but only at the cost of assuming extremely high levels of nontiming response generation in animals such as turtles. For this reason, it may be more plausible to suggest that different species do differ in timing sensitivity. Our model furthermore predicts, in accordance with most data, that obtained coefficients of variation will increase with FI value, and relates different patterns of increase to different degrees of susceptibility to nontiming response generation. This process must operate with low probability per unit time in animals such as cats, and the steep increase in obtained coefficient of variation with increases in FI value in some other animals suggests a much higher level of nontiming response generation. Note that, within a species, we can assume that the scalar property of constancy of coefficient of variation as the FI value changes is applicable. The model finally suggests that different species probably differ both in timing sensitivity and in the degree of nontiming control. Described more loosely, animals such as cats can time well and inhibit nontiming responses; animals such as turtles can do neither of these things.

It should be acknowledged that the exact form of the function relating measured coefficient of variation to FI value depends both on the probability of nontiming response generation (as illustrated in the lower panel of Fig. 8) and also on assumptions about the way in which response rates generated by the hypothesized timing process vary as the FI varies. In the model above, for simplicity we have assumed that the Gaussian growth function expressing the contribution of the timing process peaks at the FI value as this is varied, which is equivalent to assuming that overall response rate on FI declines roughly linearly with increases in the FI value. This assumption may be unrealistic (Lowe *et al.*, 1979), but it is important to note that the contribution of the type of nontiming process described above to increases in coefficient of variation with increasing FI will be the similar for any monotonically declining function relating response rate generated by timing to FI value. The prediction of *absolute* response rates on FI, as opposed to relative response frequencies in different parts of the interval, appears to have been somewhat neglected in analyses of temporal regulation under this schedule (Killeen, 1979, is a notable exception). This contrasts markedly with the situation for aperiodic interval schedules, where changes in absolute response rate as a function of schedule value have received extensive analysis (see Herrnstein [1970], McDowell & Kessel [1979], and Wearden & Clark [1989] for just

three among many alternative approaches). A model predicting absolute response rate on FI as well as response distribution within intervals and features such as the postreinforcement pause is presently lacking, and this lack contributes to difficulties in understanding the way in which measures such as the coefficients of variation measured from data and shown in Fig. 1 to 6 change with the FI value.

There are two other problems which exist for our model. One is the results from doves and pigeons trained by Lejeune and Richelle (1982), which show declining coefficients of variation as FI values increase. Our model, in its simple form, is unable to account for such declines, except by assuming that the probability of nontiming response generation within intervals actually declines as the interval grows. While such a decline may be compatible with certain incentive-like ideas (e.g., Gibbon & Balsam, 1981) it seems a somewhat arbitrary device in the present context.

The second-main problem is that our model, while offering a framework for integrating certain trends in data, is difficult to directly test. For example, two differing coefficients of variation derived from response functions may differ because (i) underlying timing sensitivity differs while nontiming response probability is the same, (ii) nontiming response probability is the same while underlying timing sensitivity varies, or (iii) both processes are different. Multiprocess models like the one advanced here make it extremely difficult to evaluate theories such as scalar timing, since measures of behavior such as coefficients of variation cannot be taken at their face value, and can almost always be reconciled with an underlying scalar process, even though at first sight they may appear to contradict scalar theory.

The Comparative Psychology of FI Responding: Some General Considerations

The fact that different methods have to be employed with different organisms even on "standard" behavioral tasks such as FI schedules clearly poses problems of interpretation of obtained results. Response manipulations differ across the range of species discussed above, as do reinforcer type and (presumably) magnitude, as well as motivational states. The particular difficulties of working with "lower" species such as fish, crabs, flies, and worms have been discussed elsewhere (e.g., Bitterman, 1960, 1965); in the present context, the principal methodological question is whether the interspecies differences in our chosen measure of performance under the FI schedules (i.e., the coefficients of variation shown in Fig. 7) actually reflect different behavioral capacities of the different species, or whether they result wholly or partly from inadequate methodology. As Bitterman (1960, 1965) points out, probably the safest form of interspecies comparison involves functional relations, that is, an examination of whether different species behave similarly when some experimental

condition is systematically changed. Performance in a single experimental condition can be both uninformative and misleading.

Considering the body of experimental data analyzed and discussed above, we can observe cross-species similarities in two sorts of functional relation. One is the relation between average response relative frequency and time in the FI, represented in our analyses by the shape of the response frequency versus interval bin functions (e.g., Fig. 1). All the species we discuss (with two possible exceptions) generally manifest an approximately Gaussian response frequency increase with elapsed time in the FI interval. For example, Gaussian curves provide good fits to data from monkeys and cats (Fig. 1) as well as fish (Fig. 5). Examination of cumulative records (e.g., Dews, 1978; Lejeune, 1971; Lejeune & Richelle, 1982; Lowe & Harzem, 1977) further supports the conclusion that a wide variety of animal species clearly exhibits temporal differentiation of responding within FI intervals. Furthermore, the Gaussian response frequency versus time in the interval function continues to hold as the FI value changes in most species considered above for which we have data.

The two possible exceptions to the cross-species similarity noted above are turtles and, perhaps more surprisingly, turtle doves. As mentioned in previous sections, evidence for well-regulated response frequency versus time functions from FI intervals from these species appears markedly weaker than for others (as manifested in the high coefficients of variation shown in Fig. 4 and 6). In the case of turtles, it seems likely that methodological inadequacies played some role in generating the poor temporal control found (for another experiment with a similar species, see Pert & Gonzalez, 1974), although it is still possible to assume that organisms such as turtles do differ fundamentally from mammals in some behavioral capacities (e.g., Bitterman, 1965; Pert & Gonzalez, 1974). The performance of turtle doves (Lejeune & Richelle, 1982) is more mysterious, since although these subjects are obviously closely related to pigeons and were run under apparently identical experimental conditions to pigeons in Lejeune and Richelle's study, their performance under FI was different from that of pigeons. Whatever the explanation of the striking differences in degree of temporal control found from pigeons and turtle doves under FI, the results do illustrate an important point that the performance of closely related species on standard tasks will not always be very similar (although in some cases it is; see, for example, coefficients of variation from rats and woodmice shown in Fig. 7).

The other functional relation manifested by most of the species used in our article is, as noted above, an increase in response function coefficient of variation with increases in FI value. In this case, this increase is exhibited by cats, rats, mice, Lowe and Harzem's (1977) pigeons, Tilapia, and turtles, with only Lejeune and Richelle's (1982) pigeons and turtle doves representing exceptions. Overall, however, the results pre-

sented above do suggest that two cross-species commonalities do hold when FI performance is considered.

Another methodological issue affecting all studies of behavioral adaptation in different species is that one can never be sure that the technique used has accurately assessed the full capacity of the subject. In the case of temporal regulation, if subjects possess a timing mechanism with a certain sensitivity which is used to time behavior, at best, behavioral measures can give only an imperfect indication of that sensitivity. Performance of animals can be worse than the precision of any internal clock they possess, if for example subjects produce a proportion of responses not controlled by a timing mechanism, but cannot be better. In a standard schedule situation such as FI, performance in terms of coefficient of variation measures generally seemed to improve with increased schedule exposure, although it is impossible to decide whether sufficient schedule exposure has been given for behavioral capacity to be properly assessed.

Within a single species such as the pigeon, changing the response used as a manifestation of temporal regulation can markedly affect the conclusions drawn about timing capacities. For example, two studies of pigeons' performance on temporal differentiation schedules (Jasselette, Lejeune, & Wearden, 1990; Lejeune & Jasselette, 1986) found much greater precision of temporal regulation exhibited if a *perching* response was used, rather than the more common key-peck operant. One possible reason for this is that the key-peck may be more subject than the laborious perching response to control by nontiming factors, such as elicitation by illuminated response keys (see discussion in Jasselette *et al.*, 1990). However, FI performance may be less affected by changing the operant, as in the study by Lejeune and Jasselette (1985). Here, the same pigeons were trained under FI 60 s with a key-pecking and a treadle-pressing operant, and neither postreinforcement pause nor index of curvature values were systematically altered by change of response. Absolute response rate was, however, always higher with the key-peck response. However, in spite of the apparent robustness of indices of temporal control on FI (such as pause and curvature index) to changes in the operant in the Lejeune and Jasselette (1985) study the possibility remains that some different procedure, response, or schedule condition might suggest that the capacity for temporal regulation in species such as fish, turtles, and turtle doves is greater than is implied by their performance on FI schedules.

We will finally briefly attempt to put the results presented above in the general context of the comparative psychology of learning, whose long and complex history has been reviewed previously (Bitterman, 1960, 1965; Demarest, 1983; Gottlieb, 1984; Hodos & Campbell, 1969; Yarczower, 1984; Yarczower & Hazlett, 1977). Although, in general, results suggest a deterioration in temporal control under FI as we move from higher

organisms such as monkeys and cats to lower ones such as fish and turtles (e.g., Fig. 7), such conclusions must be viewed with caution if we are interested in the evolution of temporal regulation of behavior, as the species considered are not related to each other in any proper evolutionary line (Hodos & Campbell, 1969). Differences in temporal regulation, however, may make sense within another perspective which transcends phyletic and cladistic ordering and rather focuses on trends in behavioral plasticity and versatility. Within this perspective, which is labeled *anagenetic* (Rensch, 1947) different grades or levels can be distinguished (Schneirla, 1949) on the basis of criteria such as behavioral adaptability, ontogenetic plasticity, and independence from the environment. Anagenesis can be generally defined as the progressive upward evolution of adaptive behavior or intelligence (Demarest, 1983; Gottlieb, 1984). Anagenesis transcends ecological variables not because it ignores them but rather because it is concerned with the range of behavior that animal subjects can reveal when faced with challenges different from those encountered in their natural environment. As Gottlieb (1984, p. 449) puts it "a grade is a particular level in a series of improvements on any structural or functional unit of analysis, in which groups may or may not be closely related from a genetical standpoint." Valuable comparative research within the anagenetic perspective has to be grounded on knowledge of the sensori-motor capacities of the species under study, as well as on its species-typical behavioral repertoire.

Suggestions made by Bitterman (1960, 1965) or Gottlieb (1984), among others, clearly indicate methodological guidelines which might be followed in anagenetic studies: compare closely and distantly related species, submit species to experimental alterations of the species-typical ecology, and challenge them with species-atypical tasks. Bitterman (1960) further suggests controlling sensori-motor and motivational variables by their systematic variation. That is, since it is impossible to equate these variables between species on the basis of some arbitrary criterion, a better strategy is to vary them over a range, and to observe whether between-species differences in behavior still occur. A comparative psychology of learning within the anagenetic framework also requires that the species be submitted to an array of tasks which differ in complexity, so as to avoid conclusions based on artifactual differences (Bitterman, 1965).

Within the study of temporal regulation of behavior, it is not clear that procedures such as the peak procedure, FI, or temporal differentiation schedules can be reliably classified in terms of their complexity. Perhaps a more valid type of anagenetic analysis of cross-species differences in temporal regulation might be obtained from examination of behavior in situations in which temporal features of the task vary rapidly (as in cyclic FI for example; see Innis & Staddon, 1971). Transitions from one schedule

parameter value to another, or from one schedule type to another, might also have useful analogies with reversal learning situations, such as those studied in a comparative context by Bitterman (1960, 1965).

The experimental data presented above, like almost all others ever obtained, are a long way from matching anagenetic methodological requirements. Nevertheless, in our results, adaptability in the anagenetic sense may be manifested in the ability to distribute behavior nonrandomly within time periods, in accordance with previously experienced temporal environmental characteristics such as inter-reinforcer interval. In the data presented here, always remembering the reservation that only one schedule type was used, adaptability to temporal regularities does increase from turtles to fish, then to pigeons, then to rats and mice, and on to cats and monkeys. Considering a yet wider range of species, there is other evidence that adaptability to FI schedules varies markedly. At one extreme, Grossman (1973) reported no evidence of temporal regulation in honey bees under FI on the basis of inspection of cumulative records; at another, human adults who use chronometric counting to regulate their performance on FI schedules may respond just once or twice at the end of the interval (Lowe, 1979), a precision of adjustment to the temporal regularities of FI finer than that exhibited by nonhuman species.

Overall, our analyses suggest that some important questions about timing of behavior, both within and between species, can be addressed by a quantitative examination of FI performance. Although FI schedules may be impossibly complicated from an associationist point of view (Jenkins, 1970; Mackintosh, 1974) they may still provide a valuable technique for investigating the nature and mechanisms of temporal control in animals. The application of scalar timing theory to FI responding also provides a framework for interspecies comparisons, whether or not the theory fits data perfectly in its simple form. A persistent problem with comparative studies of performance on learning tasks is the difficulty of drawing conclusions more general than the obvious result that species which are biologically very different behave differently. Bitterman (1965) attempted to generalize results from discrimination learning experiments principally by classifying different animal species in terms of the similarity of their behavior to "prototype" behavior of rats and fish. More recently, Wasserman (1981) has argued that the study of animal cognition can provide a framework for a renaissance of comparative psychology. Our work is obviously in sympathy with Wasserman's argument, as a theory of the processes which might be underlying FI performance, even if this theory is imperfect, as well as the uniform data analysis technique that this theory provides, offers structure to interspecies comparisons.

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