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Multiple-Interval Timing in Rats: Performance on Two-Valued Mixed Fixed-Interval Schedules

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Three experiments studied timing in rats on 2-valued mixed-fixed-interval schedules, with equally probable components, Fixed-Interval S and Fixed-Interval L (FI S and FI L, respectively). When the L:S ratio was greater than 4, 2 distinct response peaks appeared close to FI S and FI L, and data could be well fitted by the sum of 2 Gaussian curves. When the L:S ratio was less than 4, only 1 response peak was usually visible, but nonlinear regression often identified separate sources of behavioral control, by FI S and FI L, although control by FI L dominated. Data were used to test ideas derived from scalar expectancy theory, the behavioral theory of timing, and learning to time.

For more than 60 years, since its development by Skinner (1938), the fixed-interval (FI) schedule of reinforcement has been used in the study of temporal control in animals. On a simple FI schedule, the first response occurring at some particular time, *t*, in seconds after the previous reinforcer delivery is itself reinforced, and this reinforcer delivery starts the next interval of the schedule. After a period of training, animals exhibit temporal control of responding, in the sense that their responding varies markedly as a function of elapsed time in the interval. Reinforcer delivery initiates a postreinforcement pause (Lowe, Harzem, & Spencer, 1979), and when the pause finishes, subsequent responding either gradually accelerates to reach its maximum rate just before the next reinforcer delivery (Dews, 1978) or proceeds at a high, steady rate until reinforcer delivery (Schneider, 1969). When data from a number of intervals of FI are aggregated together, average response rate increases as a function of elapsed time in the interval in almost all animal species tested (Lejeune & Wearden, 1991), including mice, fish, and turtles, as well as the more conventional rats and pigeons. This response rate increase usually takes the form of the left half of a Gaussian curve, with the peak located at the FI value (Lejeune & Wearden, 1991).

Although originally developed within the behavior-analytic framework of emphasizing relations between observed behavior and imposed environmental constraints rather than analysis in terms of internal processes, FI schedules and their variants like the peak-interval procedure (Church, Meck, & Gibbon, 1994; Roberts, 1981) have recently been used extensively to test theories of timing like scalar expectancy theory (SET; Gibbon, Church, & Meck, 1984), the behavioral theory of timing (BeT; Killeen & Fetterman, 1988), and an elaboration of ideas similar to those of BeT by Machado (1997), an account subsequently called the learning to time model (LeT; Machado & Guilhardi, 2000).

One example of the application of ideas derived from SET to simple FI schedules comes from Lejeune and Wearden (1991). As mentioned above, they analyzed data from different species on FI schedules and fitted Gaussian curves to the function relating response rate to elapsed time in the interval. The spread of the curve, that is, whether response rate grew gradually throughout the interval or was concentrated at the end of it, could be measured by the standard deviation of the fitted Gaussian curve, and the standard deviation can be divided by the mean (effectively the peak location) of the curve to yield a coefficient of variation statistic. SET requires that coefficients of variation remain constant as the interval timed varies (this is a form of the *scalar property* of variance, which gives the theory its name), and Lejeune and Wearden found that there was a large duration range over which this was true for most animal species studied. In addition, the coefficient of variation, effectively a measure of temporal sensitivity where lower values indicate higher sensitivity, varied systematically with species, being lowest in cats, rats, and mice; higher in birds; and highest of all in fish and turtles. The more complex peak-interval procedure has also been used frequently to test SET (see Church et al., 1994, for only one example among many).

The present article is concerned not only with the timing behavior of rats on single FI schedules, but, more interestingly, on mixed-FI schedules where the two FI values making up the mixed schedule are equiprobable. On a mixed-FI schedule with two components, reinforcers are available either after the shorter value in the mixture or after the longer value, for example, after 30 s or 240 s, as in the present Experiment 1. Stimulus conditions in the interval remain constant, so at the start of the interval nothing signals to the animal which FI value is in force, and in our experiments, and most others, the different FI values are intermixed at random.

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Why should performance on mixed-FI schedules be of any particular theoretical interest? Leak and Gibbon (1995, pp. 3–6) provided an initial answer to this question, principally in terms of potential differences between the predictions that SET and BeT make about mixed-FI performance. SET explains timed behavior in terms of an interaction of clock, memory, and decision processes and requires that behavior exhibit the scalar property. For simple FI schedules, the coefficient of variation should remain constant as the interval timed varies. In the case of mixed-FI schedules, the timing of the intervals in the mixture should also have scalar properties: For example, in mixed FI 30 s FI 240 s, a condition used in our Experiment 1, the timing of the 30-s component and the 240-s component should be controlled by a process with the same coefficient of variation.

In contrast, BeT derives timed behaviors that are experimentally observed, such as key pecks and lever presses, from a sequence of adjunctive states, which are themselves usually unobserved. Transition from one state to another is governed by pulses from a Poisson pacemaker, but the scalar property normally found in behavior is reconciled with the principles of BeT by requiring that the pacemaker rate vary with the rate of reinforcement (effectively the FI value on simple FI schedules), such that the number of adjunctive states underlying different intervals remains the same. So, for example, if the animal traverses *n* states when timing 30 s, it should also traverse, considerably more slowly, the same *n* states when timing 240 s.

When a mixed-FI schedule is used (e.g., mixed FI 30 s FI 240 s), the number of states traversed in the entire interval presumably reflects the reinforcement rate in this condition (which is, of course, lower than that obtaining on FI 30 s alone but higher than that on FI 240 s alone). The critical point is that both the shorter FI of the mixture and the longer one are timed by the same Poisson pacemaker, so the Poisson character of the process should manifest itself in terms of more precise timing at the longer FI than at the shorter one (e.g., a smaller coefficient of variation for the 240-s component than for the 30-s one). In general, mixed-FI schedules enable the timing of a consistent duration (e.g., a constant component in the mixture) to be observed, while the other component, and thus the rate of reinforcement, changes. BeT relates pacemaker rate to the "temporal context" (Beam, Killeen, Bizo, & Fetterman, 1998) in which the animal finds itself, and it seems, at first sight, that in mixed-FI schedules, because all stimulus conditions remain constant, the temporal context for timing both components of the mixed FI must be the same. However, as is usual in attempts to distinguish BeT and SET by "critical" experimental predictions, the situation may not be as clear as it first appears, as we will discuss later.

Leak and Gibbon (1995) used a number of mixed-FI schedules, including those with two- or three-component schedules, to evaluate the relative predictions of SET and BeT and generally found support for SET. Our experiments, although relevant to the SET versus BeT issue, have the broader aim of trying to understand more generally what factors govern timing on mixed-FI schedules with two components. Some of the issues discussed are similar to those treated by Leak and Gibbon, for example, how does timing vary when the intervals making up the mixture are close together or far apart? Others, however, are rather different, in particular our attempts to understand how the contributions of the components that make up the two-valued mixed-FI schedule are combined together to produce the behavior observed. The general problem of timing of behavior on two-valued mixed-FI schedules is also discussed by Machado (1997), as part of the exposition of a complex model that deals with performance on a number of timing tasks. Machado's LeT not only predicts patterns of temporal control on FI-like schedules, but also deals with the question of how response rates should change as time passes in the schedule conditions and what response rates in the different components of the mixed-FI schedule should be.

Machado's (1997) model has marked similarities to BeT. The timing of a duration by an animal is assumed to be initiated by some time marker; in the case of FI and mixed-FI schedules, this will be the delivery of the food that terminates one interval and starts the next one. The time marker initiates a sequence of behavioral states (like the states of BeT, these are unobserved). As time passes, each state increases and then later decreases in activation level, and at time *t*, the active state can be different from one trial to another. The states not only have patterns of increasing and decreasing activation over time, but also have different degrees of association ("links") with the operant response that is measured in the experiment. When a reinforcer is delivered after a response, the state currently active increases the strength of its associative link with the response, and the extent of the increase in association depends on the activation level of the state. Absence of reinforcement during a state, on the other hand, decreases that state's association with the response, again according to how active the state was during this extinction period. The rule for generating operant responses is simply that the response rate at time *t* depends on the product of the activation level of the states active at time *t* and the values of their associative links with the response (see Machado, 1997, pp. 242–244, for a complete description). No responding will occur if (a) the currently active state(s) has no associative link with the response and (b) the states that do have associative links with the operant response are not currently active.

Machado's (1997) model deals with a number of phenomena, such as acquisition of temporal control on FI schedules (Figure 8, p. 247), which are beyond the scope of other timing models like SET and BeT, and overall has a number of complexities beyond the scope of the present article. However, one important question is why mixed-FI schedules are interesting tests of this model. To answer this, we give here a simplified exposition of arguments from Machado (pp. 251–254).

Consider a two-valued mixed-FI schedule, for example, mixed FI 30 s FI 240 s. Here, reinforcers are delivered for responses approximately 30 s or 240 s after the food delivery that starts the interval. One obvious prediction is that responding should be observed at around these times, as the states active at 30 s and the (different) states active at 240 s will have their associative links with the response strengthened by reinforcer delivery, so when these are subsequently active, responding will occur. However, in terms of consistency of reinforcement, the schedule is asymmetrical with respect to the associative changes of the states active at 30 s and 240 s. In the "short" interval of the mixed FI (30 s), the states active at around 30 s will strengthen their associative links, but the reinforcer delivered at 30 s will have no effect on the associative links of states that would later be active at 240 s, so these links are unchanged. During the "long" interval (240 s), on the other hand, the states that would be active at around 30 s become active early in the interval, but are followed by extinction, so their association with the operant response diminishes during these long intervals. In contrast, the states active at the end of the

240-s period maintain their association with the operant response by virtue of the fact that they are reinforced but never extinguished. The consequence of this is that response rates at the end of the long interval should always be higher than those at the time of the short interval. In our example (mixed FI 30 s FI 240 s), we would expect a peak in responding at around 30 s, but an even higher peak at 240 s, in those intervals where the FI 240-s schedule is in force. This prediction is easily tested in our data by measuring the peak response rates at the two times of potential reinforcement in the mixed-FI schedule.

In the present article, we describe data from what was originally conceived of as a series of five experiments, although the studies are grouped together as three separate experiments to save space. In all experiments, rats timed either simple FI schedules or two-valued mixed-FI schedules, where the two components were equiprobable and presented at random within the experimental session. Experiment 1 examined data from conditions timing FI 30 s and FI 240 s separately, then using a mixed-FI condition with these schedules as components, essentially a test of the principles for distinguishing between SET and BeT outlined by Leak and Gibbon (1995) in their Figures 1 and 2 and in an experiment similar to their Experiment 2.

Our Experiment 2 involved conditions where a single component (either FI 60 s in Experiment 2a or FI 120 s in Experiment 2b) was kept constant, whereas the other component in the mixture varied, from values below the constant component to values above it. This enabled us to examine performance on schedules where the two FI values were different (e.g., mixed FI 20 s FI 60 s) or similar (e.g., mixed FI 60 s FI 80 s). Leak and Gibbon (1995) also addressed the issue of what temporal control looks like from some schedules of this type. Finally, Experiment 3 examined performance on schedules where the shorter component of the mixed FI was constant, whereas the longer value varied (Experiment 3a) or vice versa (Experiment 3b).

Although our data have not been published previously and were derived from completely normal experimental procedures, they have the unusual characteristic that they were collected nearly 25 years ago as part of the doctoral work of Whitaker (1980). This means that the data predate both the information-processing version of SET (first published in the early 1980s, e.g., by Gibbon et al., 1984, and Church & Gibbon, 1982), BeT (Killeen & Fetterman, 1988), and LeT (Machado, 1997) as well as other recent theories (e.g., Staddon & Higa, 1999). The only negative consequence of the age of our data is that we do not have some behavioral measures that might be desirable (e.g., the start−stop−spread analysis of individual trials, proposed for the first time by Gibbon & Church, 1990, and used by Leak & Gibbon, 1995), nor can these more modern measures of performance now be derived from our data set. On the positive side, what we do have, as will be seen later, is the most extensive data set known to us on the timing of multiple intervals by animals, a data set that is not only very orderly, but which can be directly related to issues in modern theories of timing in animals.

Finally, some terminological issues. When we discuss two-valued mixed-FI schedules, we will consistently refer to the lower FI value in the mixture as *FI S* and the higher one as *FI L*: So, for example, we might consider effects of the L:S ratio on timing behavior, as in Experiments 2 and 3. Leak and Gibbon (1995) referred to mixed-FI schedules as an example of *simultaneous* timing. It seems to us that this description carries considerable surplus meaning because of its implication that the animals are timing more than one interval at the same time. Some experiments in which humans participate almost certainly involve simultaneous timing in this sense (e.g., Brown & West, 1990; Penney, Gibbon, & Meck, 2000, Experiment 1), but it is less clear that a mixed FI does, or at least always does. Consider the data in the bottom panel of Figure 1, which come from our Experiment 1 (and are similar to data presented in Leak & Gibbon, 1995, Figure 4, p. 6). Here, FI S is 30 s, and FI L is 240 s. At some elapsed time in the interval considerably greater than FI S (100 s, say), it is not necessarily the case that the animal is doing anything other than timing FI L, as the elapsed time is presumably highly discriminable from FI S, which has long passed. On the other hand, early in the interval, it is possible (although not logically necessary) that the animal is timing both FI S and FI L (e.g., at an elapsed time of 10 s), so timing may sometimes be simultaneous and sometimes not. We will just refer to timing on mixed-FI schedules as *multiple* timing, without any implication of simultaneity. What the implications of this possible nonsimultaneity of timing are for predictions about behavior will be discussed later.

Experiment 1

Experiment 1 is the simplest in our series. Rats received FI 30 s alone, FI 240 s alone, and mixed FI 30 s FI 240 s, with both intervals equiprobable, and randomly intermixed in the experimental session, as they were in all the experiments we report. We were interested in a number of issues. One was whether the scalar property of constant coefficient of variation would be manifested in our single FI conditions. The second was what timing on the mixed schedule would look like: In particular, would the timing of the FI S and FI L also show scalar properties? If the scalar property was found in the mixed condition, then, as mentioned above, this result is consistent with SET but contrary to the predictions of BeT, which would require more precise timing (i.e., a lower coefficient of variation) at FI L than at FI S. In addition, the response rates at FI S and FI L would enable a test of Machado's (1997) prediction that more responding should occur at Time L than at Time S.

Method

Animals. Four experimentally naive male hooded rats were housed individually with ad lib access to water. They were maintained at 80% of the weight reached in the last 5 days of free feeding and were fed supplementary food approximately 1 hr after the experimental session to maintain the 80% weight.

Apparatus. Standard LeHigh Valley experimental chambers (Model 142-25), enclosed in a sound-resistant housing (ambient noise level of 60 dB), were used. Only the right lever was operative. Reinforcers were 45-mg Noyes pellets. The experiment was controlled by a Data General NOVA computer.

Procedure. In the first session, the rats were trained to lever press by successive approximation, then allowed to obtain 60 reinforcers, with each lever press reinforced. Then they were exposed to FI 240 s (29 to 32 sessions for different rats), FI 30 s (28 or 29 sessions), mixed FI 30 s FI 240 s (50 to 53 sessions), then reexposed to FI 240 s (32 to 34 sessions), then finally FI 30 s (23 to 26 sessions). Sessions normally lasted until 60 reinforcers were obtained.

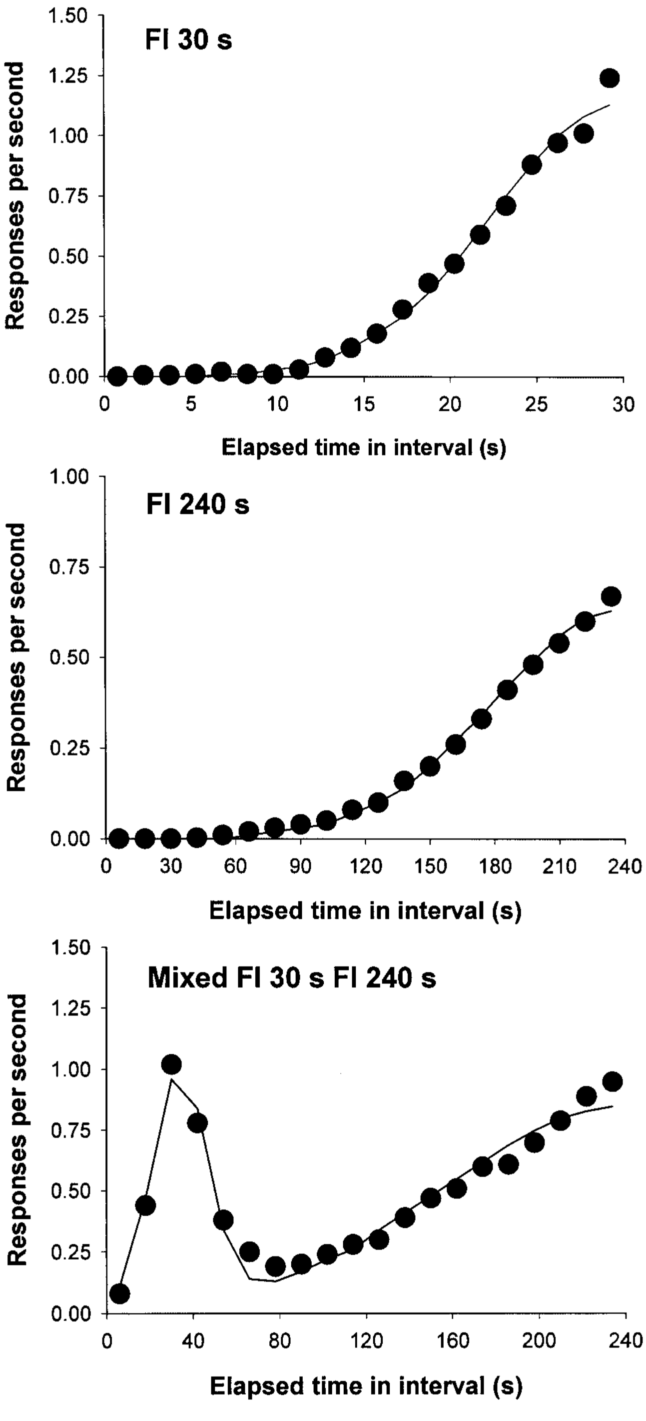

Figure 1. Response rates versus elapsed time in the interval from FI 30 s (top panel), FI 240 s (middle panel), and the FI 240-s intervals of mixed FI 30 s FI 240 s (bottom panel). Data points are shown as unconnected filled circles, and the best fitting Gaussian or two-Gaussian function is shown as a line. Parameter values for the curve fit are given in Table 1. FI = fixed interval.

Results and Discussion

Data were recorded in the form of response rate versus elapsed time in the interval. The total interval was always divided in 20 equal-length bins, so the bins were 1.5-s long for FI 30 s and 12-s long for FI 240 s. The data of interest from the mixed-FI condition come from intervals where responding according to FI L was reinforced, and bin length in these cases was also 12 s. Data were averaged over rats and over the two determinations of FI 30 s and FI 240 s and were taken from the last three sessions of exposure to the schedule in force. Figure 1 shows the response rates versus elapsed time in the interval for FI 30 s (top panel), FI 240 s (middle panel), and the FI 240-s intervals of the mixed FI (bottom panel).

Inspection of the data from the single FI conditions (top and middle panels of Figure 1) suggests that responding increased on average throughout the interval, from zero just after food to some maximum rate just before the time of food delivery. In the mixed-FI condition, responding rose toward a peak located somewhere close to FI S, then declined, only to increase again to reach a peak at FI L.

The panels of Figure 1 also show fitted curves. The curves are Gaussian curves fitted to data by the nonlinear regression program of SPSS 10 (SPSS, Inc., Chicago, IL). A Gaussian curve (G) is characterized by two parameters, its mean (or peak location), M, and its standard deviation, SD, so we will in general refer to this Gaussian function as $G(M, SD)$. To fit what is in fact a probability density function to response rates, G must be multiplied by some scaling constant, K.

When fitting Gaussian curves to the kind of data we have, one must make a number of decisions about peak location. One possibility is to force M to be at the FI value in single FI schedules, so the only parameter derived from the fit to data from these schedules, apart from the scaling parameter, K, is SD. Alternatively, the peak location, M, could itself be a parameter. When one fits data from mixed-FI schedules (e.g., data like those in the bottom panel of Figure 1), the obvious solution is to sum two Gaussian functions together, so response rate, R, is fitted by $[K_S \times \mathrm{G}(M_S, SD_S)] + [K_L \times \mathrm{G}(M_L, SD_L)]$, where K_S and K_L are scaling constants appropriate to the contribution of FI S and FI L to the response function, M_S, M_L are peak locations appropriate to FI S and FI L, and SD_S, SD_L are standard deviations for the two Gaussian curves. This is essentially the method we used, with one proviso: For single FI schedules, we always forced M to be the FI value, and for fits to mixed-FI schedules, we always forced the peak of the upper curve to be at FI L, although the position of the lower peak could vary as a parameter. The main reason this was done is that time values more than a few seconds higher than the FI value (or FI L on mixed-FI schedules) were never experienced by the animal, so if such values are found by nonlinear regression, it is impossible to interpret them theoretically. We fitted single or double Gaussian curves to averaged data (e.g., as shown in Figure 1) and also to data from individual rats. The worst fit to any sample of averaged data we analyzed had a proportion of variance accounted for (r^2) of .96, and most fits to data from individual rats had r^2 values of .95 or more, so our decision to fix the upper peak at FI L did not do violence to the data, as will be obvious from inspection of data points and curves both in Figure 1 and presented subsequently. Table 1 shows the parameter values from the curve fits to the data in Figure 1.

Consider first a comparison of the single FI schedules, FI 30 s and FI 240 s. The fitted Gaussian curve accounted for 99% of data variance, and the coefficient of variation (SD derived from the curve fit divided by the FI value) was .25 for both schedules, supporting the scalar property in timing of single FI schedules, even when absolute duration timed varied eight-fold. Also shown

Table 1
Schedule and Parameter Values From Curve Fitting Conducted on Data From Experiments 1, 2, and 3

Experiment	FI S	FI L	P S	cv S	h S	cv L	h L	r^2
1		30				.25	1.13	.99
		240				.25	0.63	.99
	30	240	33.9	.38	0.97	.35	0.85	.96
2a		60				.19	1.66	.99
	20	60	21.4	.26	0.51	.33	1.18	.98
	40	60	37.9	.14	0.14	.29	1.42	.99
	60	80	54.4	.13	0.20	.37	1.53	.99
	60	100	65.3	.28	0.74	.15	0.83	.99
2b		120				.19	0.97	.99
	40	120	42.2	.32	0.30	.43	0.72	.99
	80	120	78.4	.20	0.57	.23	1.30	.99
	120	160				.28	1.35	.98[a]
	120	200	120.9	.27	0.32	.27	0.86	.99
3a		30				.22	0.79	.99
	30	45	31.0	.15	0.18	.28	1.43	.99
	30	60	31.8	.22	1.02	.21	1.23	.99
	30	120	34.1	.22	1.01	.21	0.84	.98
	30	240	32.0	.27	1.16	.33	0.52	.97
3b	15	300	21.7	.57	0.39	.21	0.52	.96
	30	300	34.8	.40	0.43	.39	0.19	.97
	45	300	50.9	.33	0.79	.24	0.69	.97
	60	300	66.2	.32	0.63	.26	0.42	.97
	75	300	83.1	.33	0.50	.32	0.43	.96

Note. Single fixed-interval (FI) values are given as FI L only. FI S and FI L = shorter and longer FI value in mixed-FI schedule (in seconds), respectively; P S = peak location, in seconds, of fitted Gaussian curve corresponding to FI S; cv S and cv L = coefficients of variation of fitted shorter and longer curves, respectively; h S and h L = peak heights (responses/second) of fitted shorter and longer curves, respectively; r^2 = proportion of variance accounted for by the curve fit.
[a] No two-peak fit was possible.

are the peak heights derived from the curve fits, which correspond to the predicted response rate at the peak of the Gaussian curve. Peak response rate was nearly twice as high on FI 30 s than on FI 240 s, consistent with the fact that the rate of reinforcement is eight times greater in the former case than in the latter.

Consider next parameters derived from the fit to data from the mixed-FI schedule. The peak of the Gaussian curve for the corresponding to the lower FI was close to FI S (33.9 s compared with 30 s), and the coefficients of variation for the two Gaussian curves were .38 (FI S) and .35 (FI L). Peak heights from the two Gaussian curves were more similar than for the single FI conditions, although the peak was slightly higher at FI S than at FI L. The function produced by summing two Gaussian curves fitted data well ($r^2 = .96$).

Single Gaussian curves (to data from single FI schedules) and double Gaussian curves (to data from mixed-FI schedules) were fitted to data from the individual rats in Experiment 1. Parameter values are given, along with those of fits to data from all individual rats used in the present study, in the Appendix to this article. Consider first the FI 30-s and FI 240-s single schedules. For individual rats, coefficients of variation were similar in both cases, and peak heights at the end of the interval were always higher at FI 30 s than at FI 240 s. Response patterns on the simple FI schedules were virtually identical to the average patterns (top and middle panels of Figure 1), apart from differences in absolute response rate, and are not presented.

Figure 2 shows response rates versus elapsed time functions from the 240-s FI of the mixed-FI schedule for all 4 rats. Inspection of Figure 2 shows that the averaged pattern shown from the mixed-FI schedule (bottom panel of Figure 1) was representative of the performance of individual rats. For all rats, responding increased from low levels immediately after the start of the interval to a peak around FI S. Response rates then fell to low levels, before increasing to a peak at FI L. All 4 rats showed this pattern, although they differed markedly in absolute response rate (e.g., note that Subjects R14 and R15 responded about five times more rapidly than Subject R16). For 2 rats, the coefficient of variation of FI L in the mixed FI was greater than that of FI S, and for the other 2, the opposite was found. For 2 rats (R13 and R14), the peak height at S was greater than at L; for 1 rat (R15), the peak heights were almost identical; and for Subject R16, higher response rates were found at L than at S.

Overall, therefore, our data found scalar timing of behavior (i.e., constant coefficient of variation) in averaged data from the two single FI schedules and no clear deviation from scalar timing in individuals. This is consistent with both SET and BeT, as BeT produces the result by essentially varying pacemaker rate between the FI 30-s and FI 240-s schedules. In the mixed-FI schedules, the relative constancy of the coefficient of variation for FI S and FI L in the averaged data appears more consistent with the predictions of SET than with those of BeT, which would predict that the longer FI component in the mixed schedule would be timed markedly more precisely than the shorter one.

Leak and Gibbon (1995) presented only one data set (their Figure 4, p. 3, coming from an unpublished study not fully described in their article), which used a two-valued mixed FI with a

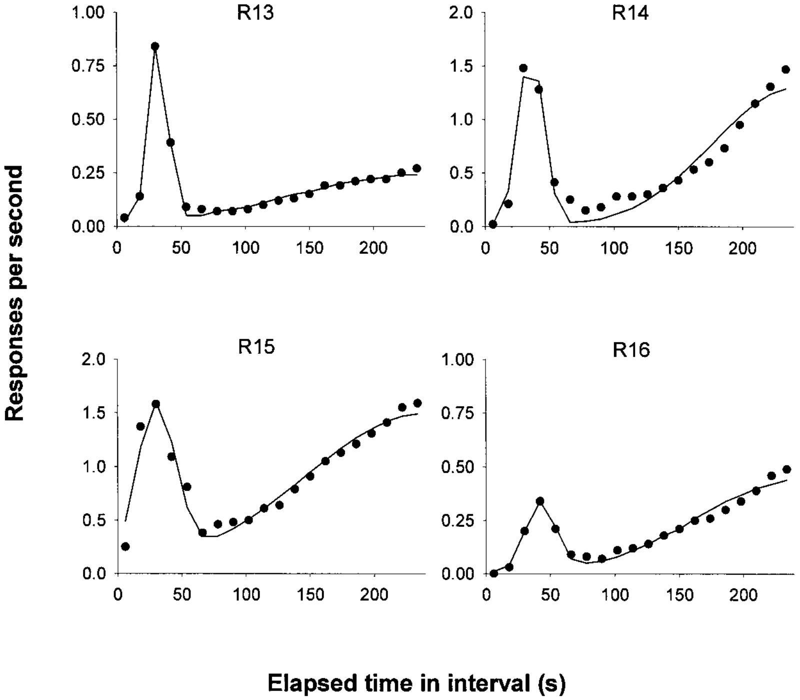

Figure 2. Data from the FI 240-s interval of mixed FI 30 s FI 240 s for individual rats (R13–R16). Data points are shown as unconnected filled circles, and the best fitting two-Gaussian function is shown as a line. Parameter values for the fits are given in the Appendix. FI = fixed interval.

large L:S ratio (12:1, from mixed FI 10 s FI 120 s), and their data resemble the results we obtained from mixed FI 30 s FI 240 s in all respects. Two peaks were clearly visible in the response rate versus time in the interval function obtained from the FI 120-s component of the mixed FI, with a period of low-rate responding between them; the peaks appeared to be centered approximately at FI S and FI L (although Leak and Gibbon did not present any quantitative analysis). The peak height at FI S was higher than that at FI L, but only about 50% higher.

Our Experiment 2 uses a more complex set of schedules and consisted of two subexperiments, which are reported together as they were procedurally and conceptually almost identical. In Experiment 2a, a FI 60-s schedule was presented alone or as a component of a mixed FI. In the mixed-FI conditions, the other component was varied over values of 20, 40, 80, and 100 s, producing L:S ratios of 3.00, 1.50, 1.33, and 1.67, respectively. In Experiment 2b, all FI values were twice as long, and the constant component was FI 120 s, presented either alone or in a mixed schedule with values of 40, 80, 160, and 200 s, respectively, which produced the same L:S ratios as in Experiment 2a.

Leak and Gibbon (1995) discussed the conditions in which two distinct response peaks (like those shown in the bottom panel of our Figure 1) will be obtained from mixed-FI schedules in terms of the L:S ratio. Catania and Reynolds (1968) reported double peaks when the L:S ratio was 4:1 or more but not when it was less, and Leak and Gibbon reported double peaks when the ratio was 8:1 but not when it was 2.5:1. However, these conclusions seem to be based on visual inspection of the response rate versus elapsed time in the interval functions, rather than on quantitative analysis. In our Experiment 2, we allowed the nonlinear regression program to decide whether there were separate contributions to the response function observed on the mixed-FI schedule from FI S and FI L, rather than simple visual inspection. As will be seen later, whenever there were two peaks obvious on visual inspection, the nonlinear regression program identified them. In addition, however, the program sometimes indicated contributions from both FI S and FI L on mixed schedules with small L:S ratios.

Experiment 2

Method

Animals. Eight male hooded rats were arbitrarily allocated to two groups of 4. One group served in Experiment 2a, one in Experiment 2b. Deprivation and housing conditions were as in Experiment 1.

Apparatus. The apparatus was the same as in Experiment 1.

Procedure. In Experiment 2a, the constant component of the mixed-FI schedules was FI 60 s, which was also presented alone. In the first session, the rats received lever-press training and then obtained 60 reinforcers, with each response reinforced. The rats were then exposed to FI 60 s (70 to 74 sessions), mixed FI 20 s FI 60 s (17 to 20 sessions), mixed FI 60 s FI 100 s (18 or 19 sessions), mixed FI 40 s FI 60 s (16 to 20 sessions), and finally mixed FI 60 s FI 80 s (16 to 19 sessions). Experiment 2b was almost identical, except that all schedule values were twice as long. After initial lever-press training, the rats received FI 120 s (72 to 75 sessions), mixed FI 120 s FI 200 s (18 to 20 sessions), mixed FI 40 s FI 120 s (23 or 24 sessions), mixed FI 120 s FI 160 s (32 to 36 sessions), and mixed FI 80 s FI 120 s (17 to 19 sessions).

Results and Discussion

Figure 3 shows response rates versus elapsed time in the interval from the mixed-FI schedules of Experiment 2a, and Figure 4

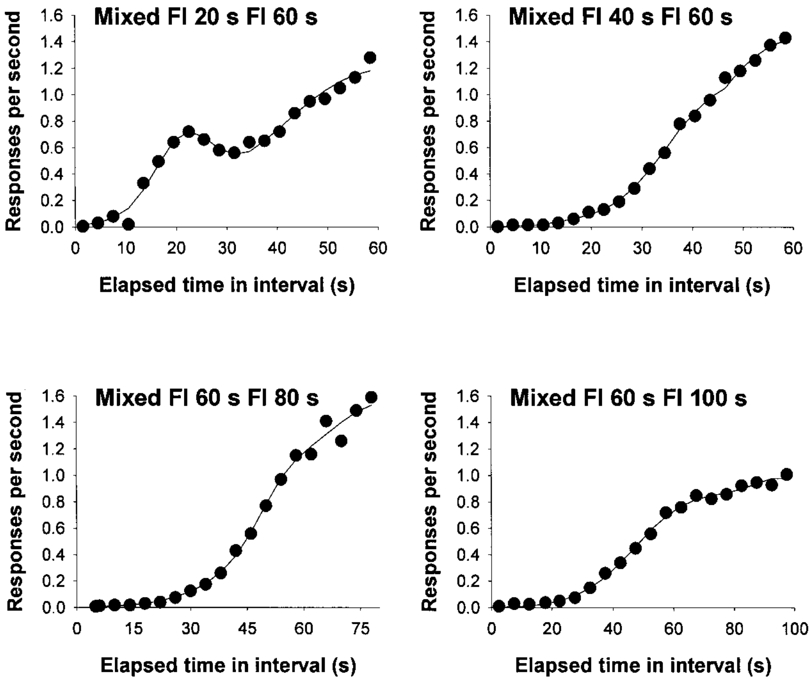

Figure 3. Response rate versus elapsed time in the interval functions from Experiment 2a. Data come from the longer component of the two-valued mixed-FI schedule. Within each panel, the values of the two components (FI S and FI L) are given. Data points are shown as unconnected circles, and the line in each panel comes from the best-fitting two-Gaussian fits described in the text. FI S and FI L = the shorter and longer fixed-interval (FI) components, respectively, of the mixed-FI schedule.

shows the same data from Experiment 2b. All of the data in these figures were derived by averaging across the 4 rats in each experiment before curve fitting. To improve the layout of the figures, we did not show data from the single FI schedules (FI 60 s for Experiment 2a, FI 120 s for Experiment 2b), but these were virtually identical in form to data from the single FI conditions of Experiment 1 (shown in the top and middle panels of Figure 1).

Consider first data from Experiment 2a (Figure 3). Visual inspection of the data suggests that only the mixed-FI 20-s FI 60-s schedule generated two obvious response peaks, but in fact the nonlinear regression program found that all of the response functions could be well fitted by the sum of two Gaussian curves, even that from mixed FI 60 s FI 80 s, where the L:S ratio was 1.33. All two-Gaussian fits were well adjusted to the data (r^2 = .98 or .99 in all cases), and parameter values are shown in Table 1. The lower peak of the two-Gaussian fit was allowed to vary, and Table 1 shows that it was always within 10% of FI S, as this varied across conditions from 20 s to 60 s. How the contributions of FI S and FI L were combined when the L:S ratio varied will be considered further below.

Figure 4 shows analogous data from Experiment 2b. Once again, visual inspection identified two peaks when the L:S ratio was large (mixed FI 40 s FI 120 s), although the regression produced two peak fits for two of the other three cases: Only the mixed-FI 120-s FI 160-s condition could not be fitted by the sum of two Gaussian curves, and here a single curve with a peak at 160 s was used.

This is the first case presented in this article in which a two-Gaussian fit could not be found for data from a mixed-FI schedule. What criteria were used to reject a two-Gaussian fit both in the present case and in the cases (discussed later) in which two-Gaussian fits could not be obtained to mixed-FI data from individual rats? A two-Gaussian fit was rejected if either one of two cases was met. The most common case was that the fit produced a negative value for the scaling constant (K_S) of the Gaussian curve corresponding to FI S: a value that is obviously meaningless. The other, less common case was that in which the peak location identified as corresponding to FI S was greater than FI L: For example, on mixed FI 30 s FI 45 s, the peak identified for the FI 30-s schedule was greater than 45 s. Both of these cases imply that control of behavior was strongly exerted by FI L, with little or no contribution from FI S, and in all the cases in which no two-Gaussian fit was possible the data were well fitted by a single Gaussian curve peaked at FI L. Table 1 shows parameter values from the fits to averaged data from Experiment 2b, and, once again, r^2 values were high (.98 or .99), and the lower peak, which was allowed to vary, was within 10% of FI S.

Our data were similar to those of Leak and Gibbon (1995) in that when the L:S ratio was small (less than 3 in our case), two response peaks were not clearly visible on inspection of response functions. However, the fact that the nonlinear regression procedure identified two underlying sources of temporal control in all but one case (mixed FI 120 s FI 160 s) enables us to examine more precisely just what does happen when the L:S ratio is low in mixed-FI schedules. The critical measure appears to be the peak height (i.e., the peak of responding predicted by the Gaussian curves).

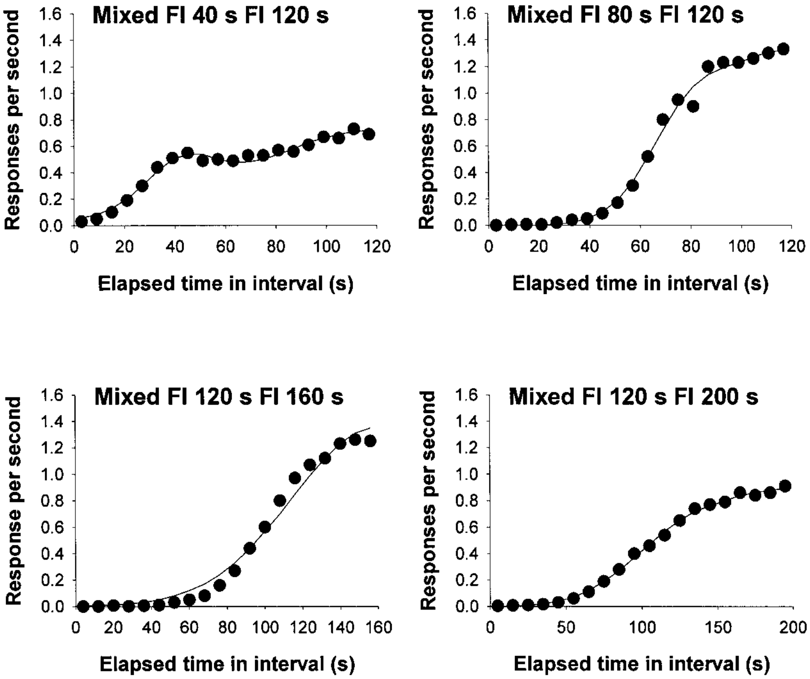

Figure 4. Response rate versus elapsed time in the interval functions from Experiment 2b. Data come from the longer component of the two-valued mixed-FI schedule. Within each panel, the values of the two components (FI S and FI L) are given. Data points are shown as unconnected circles, and the line in each panel comes from the best-fitting two-Gaussian (or single-Gaussian in the case of mixed FI 120 s FI 160 s) fits described in the text. FI S and FI L = the shorter and longer fixed-interval (FI) components, respectively, of the mixed-FI schedule.

Consider first data from Experiment 2a. In Figure 3, all of the data were well fitted by the two-Gaussian function, but the peak heights reflect the relative contributions of the curve centered around FI S and that centered on FI L. In Experiment 1, with an 8:1 L:S ratio, peak height was higher for the FI S component than for the FI L one, but when the L:S ratio was small, the reverse was the case, and the peak at FI S was always lower than that at FI L. When the L:S ratio was particularly small (1.5 and 1.33 from the mixed-FI 40-s FI 60-s and mixed-FI 60-s FI 80-s conditions), the peak height associated with the FI S component was also particularly small, and the peak height at FI L was much greater. Data from Experiment 2b (Figure 4 and Table 1) show an almost identical picture. Peak heights at FI L were always more than twice as great as those at FI S, and even data from the mixed-FI 120-s FI 160-s condition followed this same rule trivially, as the peak at FI S disappeared altogether, leaving that at FI L infinitely greater.

In general, then, when the L:S ratio was small on mixed FI (less than 3 in our studies), not only did the two-peak form of the response function disappear, even though the nonlinear regression program usually identified separate sources of control by FI S and FI L, but the balance of control of responding shifted away from FI S toward FI L, with at a limit control by FI L alone.

Data from individual rats (given in the Appendix) showed all of the trends noted in the averaged data. In Experiment 2a, two-peak fits were found in all individual rats only for mixed FI 20 s FI 60 s (L:S ratio = 3), and, conversely, only 2 rats produced a two-Gaussian fits for the mixed FI 60-s FI 80-s schedule. Peak heights at L were higher than at S for all of the conditions in which two-Gaussian fits were possible for individual animals. In Experiment 2b, likewise, two-Gaussian fits were obtained to data from all rats with a 3:1 L:S ratio (mixed FI 40 s FI 120 s), but only 1 rat (R8) produced data with a two-Gaussian fit from the condition with the smallest L:S ratio (mixed FI 120 s FI 160 s). Peak heights at L were usually higher than at S (10 out of 13 cases producing two-Gaussian fits), and in the few cases in which the peak height at S was higher than at L, the heights were very similar.

Our final study, Experiment 3, consists of two subexperiments, which differed procedurally but had the common theme of keeping one component of the two-valued mixed-FI schedule constant, while varying the other. In Experiment 3a, a FI 30-s schedule was either presented alone or as FI S, the lower component of the mixed schedule, whereas FI L varied over values from 45 s to 240 s. In Experiment 3b, FI L was fixed at FI 300 s (although this value was never presented alone), and FI S varied over the range from 15 s to 75 s.

Experiment 3

Method

Animals. Eight male hooded rats were arbitrarily allocated to either Experiment 3a (4 rats) or Experiment 3b (4 rats).

Apparatus. In Experiment 3a, four LeHigh Valley (Allentown, PA) RTC-028 operant chambers were used; all other details were as in Experiment 1. In Experiment 3b, all details were as in Experiment 1.

Procedure. In Experiment 3a, after initial lever-press training, rats received FI 30 s (30 sessions), mixed FI 30 s FI 120 s (25 sessions), mixed

FI 30 s FI 60 s (25 sessions), mixed FI 30 s FI 240 s (25 sessions), and mixed FI 30 s FI 45 s (30 sessions). In Experiment 3b, after initial lever-press training, rats received the following mixed-FI schedules: mixed FI 30 s FI 300 s (30 sessions), mixed FI 60 s FI 300 s (25 sessions), mixed FI 15 s FI 300 s (25 sessions), mixed FI 45 s FI 300 s (25 sessions), mixed FI 15 s FI 300 s (25 sessions), and mixed FI 60 s FI 300 s (25 sessions).

Results and Discussion

Figure 5 shows response rate versus elapsed time in the trial data from the longer intervals of the mixed-FI conditions of Experiment 3a, with data being averaged over the 4 rats before curve fitting. Data from the single FI 30-s schedule are not shown, but were almost identical in form to those shown in the top panel of Figure 1. Inspection of the data suggests that two response peaks were clearly present in all conditions except mixed FI 30 s FI 45 s, and that the peak of the lower response function was located close to FI S, 30 s. Table 1 shows results from the nonlinear regression analysis. As for Experiment 2a, the program found two-Gaussian fits for data from all of the mixed-FI schedules, including mixed FI 30 s FI 45 s. Inspection of the parameter values shows that (a) data were fitted well by the Gaussian (single FI) or two-Gaussian (mixed FI) functions (smallest $r^2 = .97$); (b) the position of the lower response peak was close to FI S, 30 s; and (c) peak heights for FI S were lower than those for FI L when the L:S ratio was less than 4 (with data from the FI 30-s and 45-s condition showing a particularly small peak height at FI S) but higher when the L:S ratio was 4 and 8.

Figure 6 shows averaged response rate versus elapsed time functions from the longer components of the mixed-FI schedules of Experiment 3b. Data from the repetitions of the mixed-FI 15-s FI 300-s condition were averaged together. Inspection of the data suggests that two response peaks were present in all cases. Table 1 shows the parameter values from the two-Gaussian fits that the nonlinear regression program found. Examination of the parameters showed that (a) all data were well fitted by the two-Gaussian function ($r^2 = .96$ or .97), (b) the position of the lower peak was close to FI S (although consistently about 5 s to 8 s above it), and (c) peak heights for FI S were higher than for FI L in all cases but one (mixed FI 15 s FI 300s) but were often similar in spite of the considerable difference between FI S and FI L.

Analysis of data from individual rats produced very similar results to analysis of averaged data. Consider first Experiment 3a. Only 1 rat produced a two-Gaussian fit for mixed FI 30 s FI 45 s, but data from the other rats were well fitted by single Gaussian curves peaked at 45 s. In all cases of two-Gaussian fits, the peak identified for the FI 30-s component was close to 30 s, and in most cases the peak height at S was greater than the peak height at L. Individual rats in Experiment 3b produced similar data to that shown in Figure 6. Two-Gaussian fits were obtained in all conditions, peak locations were close to FI S (although usually above FI S), and peak heights were much more likely to be higher at S than at L.

Some individual data from Experiment 3b, particularly from the mixed-FI 15-s FI 300-s condition, were anomalous, with peaks well above 15 s, and coefficients of variation for FI S, which were much higher than those for FI L. The most likely cause of the anomalies is the relatively poor temporal resolution of Experiment 3b in conditions where FI S was short. For example, in

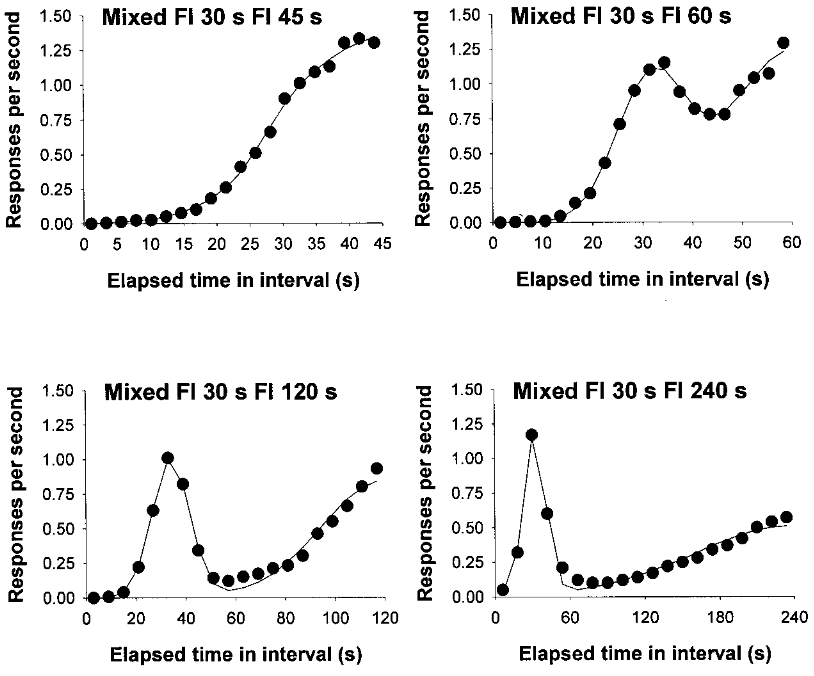

Figure 5. Response rate versus elapsed time in the interval functions from Experiment 3a. Data come from the longer component of the two-valued mixed-FI schedule. Within each panel, the values of the two components (FI S and FI L) are given. Data points are shown as unconnected circles, and the line in each panel comes from the best-fitting two-Gaussian fits described in the text. FI S and FI L = the shorter and longer fixed-interval (FI) components, respectively, of the mixed-FI schedule.

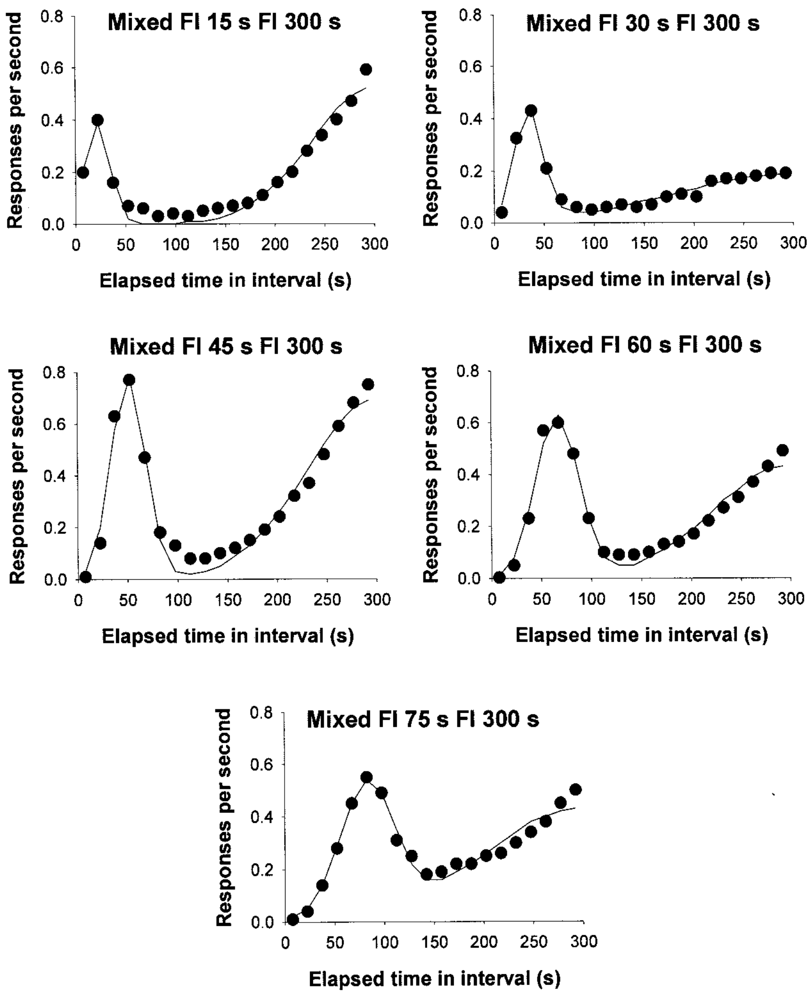

Figure 6. Response rate versus elapsed time in the interval functions from Experiment 3b. Data come from the longer component of the two-valued mixed-FI schedule. Within each panel, the values of the two components (FI S and FI L) are given. Data points are shown as unconnected circles, and the line in each panel comes from the best-fitting two-Gaussian fits described in the text. FI S and FI L = the shorter and longer fixed-interval (FI) components, respectively, of the mixed-FI schedule.

Experiment 3b, the bin width was 15 s, but in one condition FI S itself was 15 s, so measuring the peak location and coefficient of variation for this value is in all likelihood problematical and may have been the cause of the peak location being above 15 s and the coefficients of variation for the 15-s component being relatively large.

Across-Experiment Analyses

As in Leak and Gibbon (1995), some trends in our data are seen most clearly when results from the different experiments are displayed together. Figures 7, 8, and 9 show some of these. For all of these analyses, we focus on the data from individual animals.

Consider first peak location. The top panel of Figure 7 shows the location of the lower peak of the two-Gaussian function fitted to data from the different mixed-FI schedules, determined by the nonlinear regression program, as a function of the FI value that was FI S. The results shown come from individual rats, with different determinations of the same S value (e.g., 30 s in Experiment 3a) being averaged from the same rat. An anomalous value (from Subject R36 in Experiment 3b) has been omitted. Obviously the peaks located by the program tracked the FI value closely. The line shown comes from linear regression of peak location against FI value. The slope was 0.99, the intercept was 4.34 s, and r^2 was .96, confirming the impression that the peak location was located close to FI S, over the three experiments as a whole. However, the deviation between the fitted peak and FI S was not random, as the lower panel of Figure 7 shows. Peak values above the S were about three times as common as values below S, although almost all peaks were within 20% of FI S.

Consider next the coefficient of variation of the fitted curves from the different mixed-FI conditions. Figure 8 shows the ratio of the coefficients of variation from the two components of the mixed FI (that coming from FI S being divided by that coming from FI L), derived from the two-Gaussian fits to data from individual rats, plotted against the ratio of FI L and FI S. According to SET, the ratio should be 1.0 in all cases, whereas BeT would predict more

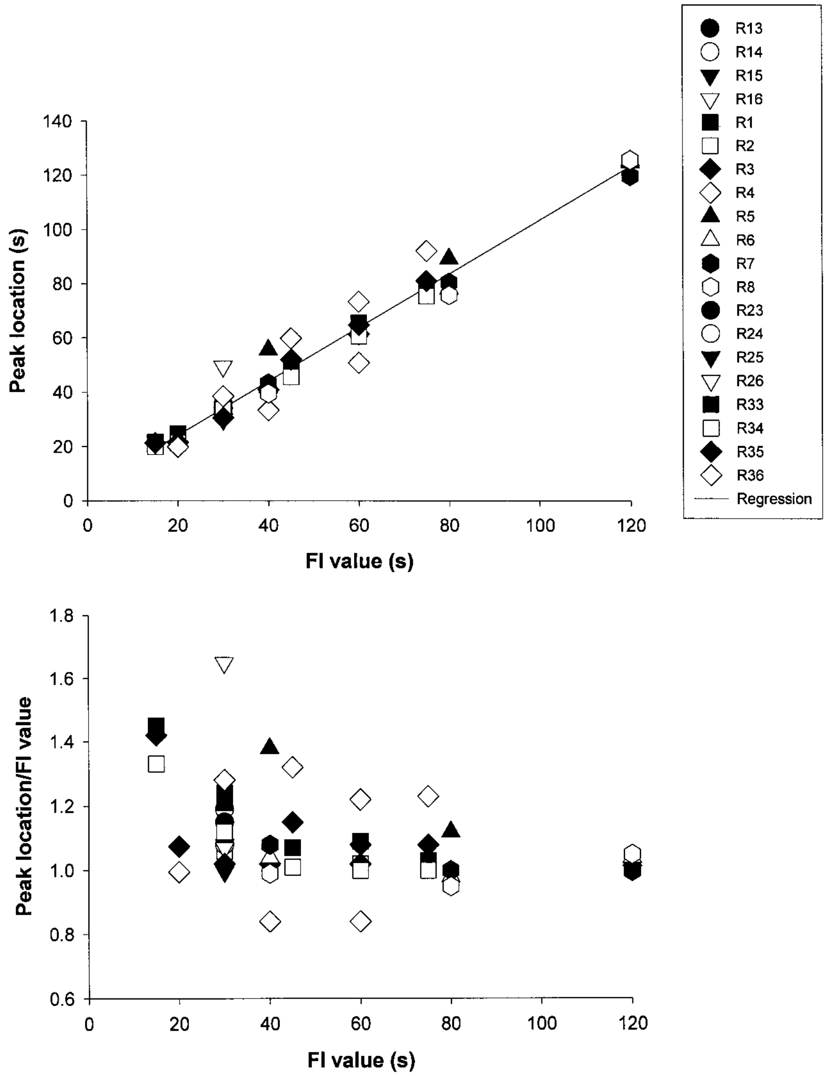

Figure 7. Top panel: Peak location (in seconds) of the Gaussian curve associated with FI S in the mixed-FI schedules used in Experiments 1–3, plotted against the FI S value in seconds. Data come from individual rats (R) where two-peak fits were obtained. The regression line for the data is shown. Bottom panel: Peak locations divided by FI S, plotted against FI S. Values above 1.0 show that peak location was above S; values below show that it was below S. FI S = the shorter fixed-interval (FI) component of the mixed-FI schedule.

precise timing of the FI L component than the FI S one (so the ratios in the top panel of Figure 8 should all be greater than 1.0).

Of the 61 cases shown in Figure 8, the coefficient of variation associated with FI S was higher than that of FI L in 29 instances, and in 32 instances the reverse was true. Inspection of the data in Figure 8 also suggests that, with the possible exception of the largest L:S ratio (coming from one condition of Experiment 3b, where the possible inflation of coefficient of variation is discussed above), there was no clear trend in coefficient of variation ratio with changes in FI values or ratios. Although the data were obviously variable from one condition and 1 rat to another, they were much more consistent with random variation around the ratio of 1.0 predicted by SET than by the higher values BeT might predict. Figure 8 shows the average coefficient of variation ratio at each L:S ratio. Although there is clear variability, probably caused in part by the fact that there are more data points at some L:S ratios than at others, the line varies apparently randomly around 1.0, at least at L:S values apart from the largest one.

Figure 9 shows the ratios of the peak heights of the Gaussian curves coming from FI S and FI L, taken from individual rats, again plotted against the L:S ratio. Here, a ratio greater than 1.0 indicates that the peak at S was higher than that at L; values less than 1.0 show the reverse. Discussion of the averaged data from the individual experiments presented previously suggested that the relative peak heights at S and L depended on the L:S ratio. When this was small (e.g., less than 3 or 4), the two intervals making up the mixed FI were close together, and the peak at L was usually higher than the peak at S. In contrast, when the L:S ratio was greater than 3 or 4, and the two intervals of the mixed FI were further apart, the peak at S was higher than at L. These effects are

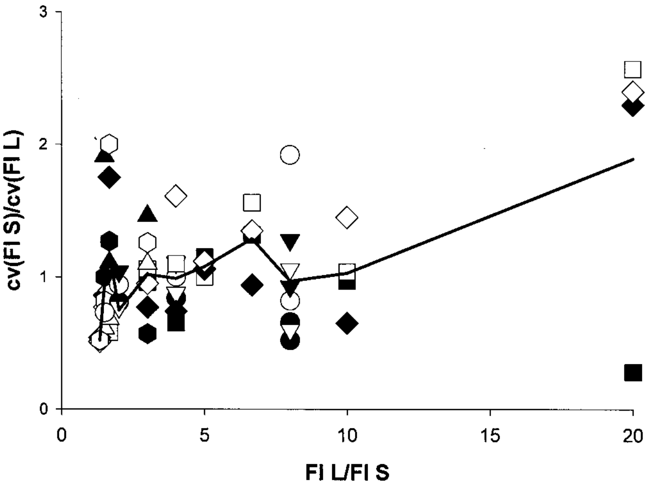

Figure 8. Ratio of coefficients of variation from two-peak fits, plotted against the L:S ratio. Coefficient of variation associated with FI S was divided by that from FI L. Values greater than 1.0 indicate that FI L was timed more precisely than FI S; values less than 1.0 indicate the reverse. Data come from individual rats (see legend in Figure 7). The line shown is the average of the points at each L:S ratio. L:S = ratio of the longer and shorter FI values, respectively, in the mixed-FI schedule; FI S and FI L = the shorter and longer fixed-interval (FI) components, respectively, of the mixed-FI schedule; cv(FI S) and cv(FI L) = the coefficients of variation of the curve fitted to data from the mixed-FI schedule.

shown very clearly in Figure 9. At the smallest L:S ratios, peak ratios were almost invariably less than 1.0 (i.e., higher peak at L), whereas as the L:S ratio grew above about 3 or 4, peak ratios were almost always above 1.0 (indicating higher response rates at S than at L). A data point from Subject R26 on mixed FI 30 s FI 240 s, where the peak ratio was 8.36, is omitted from the figure, but obviously confirms the trend noted for the peak at S to be higher than that at L when the L:S ratio was greater than 4.

General Discussion

Our results might be summarized by considering an attempt to predict performance on the longer intervals of some mixed-FI schedule mixed FI S FI L. If the L:S ratio was greater than about 4, then two peaks in the response function (one located at or near to FI S, the other located at FI L) would be obvious on visual inspection. The response curves around FI S and FI L would be of approximately Gaussian shape, with coefficient of variations that were not systematically different for FI L and FI S, and peak height at FI S would be greater (but sometimes not much greater) than that at FI L. On the other hand, if the L:S ratio was less than 4, visual inspection would not usually locate two distinct response peaks, although sources of control of responding by the separate FI S and FI L components would often be identified by nonlinear regression, at least in averaged data. When two components were identified, the contribution of FI S to the overall response function would be smaller, sometimes much smaller, than that of FI L, and peak height at FI S would usually be a fraction of that at FI L.

The dependence of behavior on mixed-FI schedules on the L:S ratio is not particularly surprising either logically or on the basis of previous work. As FI L and FI S become more similar, the animals presumably find it more difficult to maintain separate sources of temporal control, because of overlap in their temporal representations of S and L, as discussed by Leak and Gibbon (1995), who reported a similar effect of L:S ratio (as did Catania & Reynolds, 1968, before them). What is not so obvious a priori, although becomes clearer in our data, is how the "conflict" between control by FI S and by FI L is resolved when the L:S ratio is small. It is clear that, in all cases, control is more powerfully exerted by FI L than FI S. Some evidence for this comes from the single case from averaged data where two response peaks could not be identified (mixed FI 120 s FI 160 s), and here the data could be modeled by assuming control only by the longer, rather than the shorter, component of the mixed-FI schedule. In addition, all failures to find a two-peak solution for individual data (see Appendix) came from conditions where the L:S ratio was small, and in all cases a single Gaussian curve peaked at the longer FI value fitted data well.

How well do the data obtained in our study accord with theoretical predictions of SET, BeT, and LeT? Consider first peak location (Figure 7). All of the theories would predict that fitted peaks would be close to FI S and would vary with changes in S, and both of these predictions were clearly confirmed. However, the bottom panel of Figure 7 shows that peak locations were more likely to be slightly above S than below it. Why this occurs is unclear, but the effect may be of some theoretical interest if confirmed in a study with more precise temporal resolution than our own.

Consider next coefficients of variation obtained at S and L in the mixed-FI schedule. SET predicts that these should be constant, BeT that L should be timed more precisely than S (i.e., with a lower coefficient of variation), and LeT appears to make no clear predictions. Overall, our data (Figure 8) were more consistent with the predictions of SET, although data from individual rats were

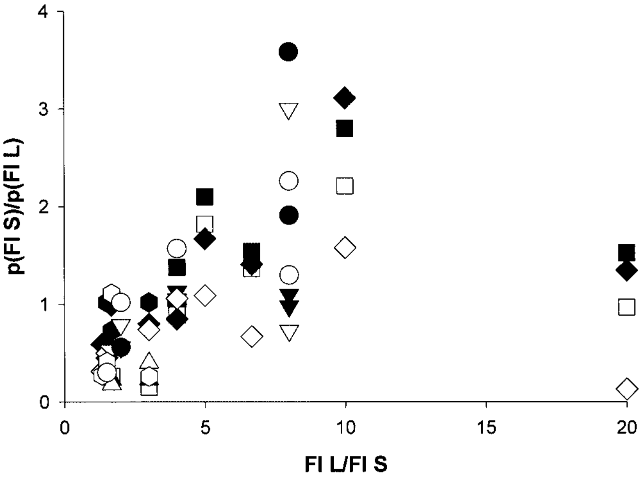

Figure 9. Ratios of peak heights derived from two-peak fits, plotted against the L:S ratio. The peak at FI S is divided by that from FI L, so values greater than 1.0 show more responding at S than L; values less than 1.0 show the reverse. Data come from individual rats (see legend in Figure 7). L:S = ratio of the longer and shorter FI values, respectively, of the mixed-FI schedule; FI S and FI L = the shorter and longer fixed-interval (FI) components, respectively, of the mixed-FI schedule; p(FI S) and p(FI L) = the peak heights of the curve fitted to data from the mixed-FI schedule.

variable. There was no trend toward more precise timing at L than at S, although, of course, individual instances of this could be found.

Finally, consider the relative response rates at S and at L. SET and BeT make no clear predictions, whereas LeT predicts that higher peak rates will be found at L than at S in all cases (Machado, 1997, pp. 251–254). Our data support Machado's prediction only for mixed-FI conditions where the L:S ratio was less than 3 or 4 (Figure 9). At higher L:S ratios, the higher peak rates were almost invariably found at S rather than at L, contrary to the predictions of Machado's model. Overall, therefore, SET seems to deal better with the patterns in our data than the other models, but sometimes only by virtue of not making any prediction at all (e.g., about peak rates), thus avoiding potential falsification. However, it should be noted that the nonsystematic difference between coefficients of variation at S and at L in data from mixed-FI schedules, which is at first sight damaging to BeT, may not in fact be so problematical for this theory.

Leak and Gibbon's (1995) interest in mixed-FI schedules as a way of distinguishing predictions of SET and BeT derives in part, as mentioned in the introduction to the present article, from the idea that the temporal context of the mixed-FI schedule, which is supposed to determine the rate of the Poisson pacemaker underlying timing according to BeT, remains constant as the intervals elapse. However, this may not be the case. For example, on mixed-FI schedules with large L:S ratios, which provide the best test of Leak and Gibbon's idea, there will almost certainly come a time in the interval that is longer than, and discriminable from, FI S, but shorter than, and discriminable from, FI L. In fact, the "dips" often found in the response rate function between S and L in our data (e.g., Figure 2) imply that there are times when the animal's expectancy of food delivery is very low, times that therefore must be discriminated from the two potential times of reinforcement, S and L.

This kind of consideration is similar to ideas from Beam et al. (1998, p. 395) and may explain how BeT can be reconciled with some of the results we obtained and some of those obtained by Leak and Gibbon (1995), which seem at first sight contrary to BeT. For example, if pacemaker rate is determined by arousal linked to expectancy of reinforcement, then on a mixed-FI schedule, this arousal may change markedly as the interval elapses. For example, put informally, the animal may begin an interval on a mixed-FI 30-s FI 240-s schedule in a high state of arousal (i.e., with high pacemaker rate), because reinforcement in a fairly short time is a 50% possibility. Later in the interval (e.g., at 60 s or 100 s after the start), arousal falls because the animal now anticipates food for certain at 240 s into the interval, but this time is remote from the current elapsed time. A fall in arousal may decrease pacemaker rate and so increases the coefficient of variation for the timing of the upcoming duration, FI L, making the coefficients of variation for the timing of S and L more similar than BeT would appear at first sight to predict, and thus more in accord with data like those in Figure 8. In general, therefore, the assumption that the rate of the BeT pacemaker will necessarily remain constant on mixed-FI schedules because the temporal context remains constant, which is the cornerstone of Leak and Gibbon's argument that mixed-FI schedules can distinguish between the predictions of BeT and SET, may not be sustainable.

The problems that some of our data pose for LeT may not be disposed of so simply. As Machado (1997) himself pointed out (p. 259), higher peak rates at FI S than FI L on mixed-FI schedules was the "greatest difficulty" that his LeT model encountered in all of the data he fitted. Machado discussed one such case from Catania and Reynolds (1968), but our study provides many more examples from conditions where the L:S ratio is greater than about 4, and here higher peak rates at S than L were virtually always found (see Figure 9). The idea of conditioning and extinction of behavioral states is central to LeT and, as discussed earlier, states active at times near S will have their associations with the response both conditioned and extinguished, whereas those active near L will only be conditioned, thus "later states are always more conditioned than earlier states . . . [so] response rate is always maximal at the end of the trial" (Machado, 1997, p. 253). It is thus difficult to see how the prediction of higher response rates at L than at S can be avoided, without substantial modification of the theory.

Our study shows the contributions that data from mixed-FI schedules can make to understanding how animals perform when reinforcers are available at two different times after a time marker and also indicate the ways in which these data can address issues relating to recent theories of timing, even if the mixed-FI schedules may not offer the critical test of predictions of SET and BeT that Leak and Gibbon (1995) supposed. Mixed-FI schedules produce orderly data both from groups and individuals, and the experimenter has complete control over the events the animals experience (unlike more complex procedures like "time-left"; see Preston, 1994), so simplifying theoretical interpretation. Our data set has limitations caused by the technology available at the time the experiments were performed, most notably in the poor temporal resolution provided in our Experiment 3b at times shortly after food delivery, but these could be easily overcome in any modern replication. Future studies of conditions like those in our Experiments 2a and 2b, where S and L were often close, and Experiments 3a and 3b, where S and L were usually far apart, if conducted with the high temporal resolution modern computing could provide, might well make important contributions to understanding empirical and theoretical aspects of timing in animals.

References

Beam, J. J., Killeen, P. R., Bizo, L. A., & Fetterman, J. G. (1998). How temporal context affects temporal production and categorization. *Animal Learning & Behavior, 26,* 388–396.

Brown, S. W., & West, A. N. (1990). Multiple timing and the allocation of attention. *Acta Psychologia, 75,* 103–121.

Catania, A. C., & Reynolds, G. S. (1968). A quantitative analysis of responding maintained by interval schedules of reinforcement. *Journal of the Experimental Analysis of Behavior, 11,* 327–383.

Church, R. M., & Gibbon, J. (1982). Temporal generalization. *Journal of Experimental Psychology: Animal Behavior Processes, 8,* 165–186.

Church, R. M., Meck, W. H., & Gibbon, J. (1994). Application of scalar timing theory to individual trials. *Journal of Experimental Psychology: Animal Behavior Processes, 20,* 135–155.

Dews, P. B. (1978). Studies on responding under fixed-interval schedules of reinforcement: II. The scalloped pattern of the cumulative record. *Journal of the Experimental Analysis of Behavior, 29,* 67–75.

Gibbon, J., & Church, R. M. (1990). Representation of time. *Cognition, 37,* 23–54.

Gibbon, J., Church, R. M., & Meck, W. (1984). Scalar timing in memory. In J. Gibbon & L. Allan (Eds.), *Annals of the New York Academy of Sciences*: *Timing and time perception* (Vol. 423, pp. 52–77). New York: New York Academy of Sciences.

Killeen, P. R., & Fetterman, G. J. (1988). A behavioral theory of timing. *Psychological Review, 95,* 274–295.

Leak, T. M., & Gibbon, J. (1995). Simultaneous timing of multiple intervals: Implications of the scalar property. *Journal of Experimental Psychology: Animal Behavior Processes, 21,* 3–19.

Lejeune, H., & Wearden, J. H. (1991). The comparative psychology of fixed-interval responding: Some quantitative analyses. *Learning and Motivation, 22,* 84–111.

Lowe, C. F., Harzem, P., & Spencer, P. T. (1979). Temporal control of behavior and the power law. *Journal of the Experimental Analysis of Behavior, 31,* 333–343.

Machado, A. (1997). Learning the temporal dynamics of behavior. *Psychological Review, 104,* 241–265.

Machado, A., & Guilhardi, P. (2000). Shifts in the psychometric function and their implications for models of timing. *Journal of the Experimental Analysis of Behavior, 74,* 25–54.

Penney, T. B., Gibbon, J., & Meck, W. H. (2000). Differential effects of auditory and visual signals on clock speed and temporal memory. *Journal of Experimental Psychology: Human Perception and Performance, 26,* 1770–1787.

Preston, R. A. (1994). Choice in the time-left procedure and in concurrent chains with a time-left terminal link. *Journal of the Experimental Analysis of Behavior, 61,* 349–373.

Roberts, S. (1981). Isolation of an internal clock. *Journal of Experimental Psychology: Animal Behavior Processes, 7,* 242–268.

Schneider, B. A. (1969). A two-state analysis of fixed-interval responding in the pigeon. *Journal of the Experimental Analysis of Behavior, 12,* 667–687.

Skinner, B. F. (1938). *The behavior of organisms.* New York: Appleton-Century-Crofts.

Staddon, J. E. R., & Higa, J. (1999). Time and memory: Towards a pacemaker-free theory of interval timing. *Journal of the Experimental Analysis of Behavior, 71,* 215–251.

Whitaker, J. S. (1980). *Temporal control of animal operant performance.* Unpublished doctoral thesis, University College of North Wales, Bangor, Gwynedd, United Kingdom.

Appendix

Schedule and Parameter Values From Curve Fitting Conducted on Data From Individual Rats in Experiments 1, 2, and 3

Experiment	Rat	FI S	FI L	P S	cv S	h S	cv L	h L	r^2
1	13		30				.24	0.60	.99
			240				.28	0.22	.99
		30	240	32.4	.22	0.86	.42	0.24	.99
1	14		30				.27	1.99	.99
			240				.22	0.99	.99
		30	240	35.7	.50	1.65	.26	1.28	.94
1	15		30				.21	1.55	.97
			240				.27	0.77	.99
		30	240	29.9	.50	1.48	.39	1.50	.94
1	16		30				.22	0.49	.93
			240				.23	0.34	.99
		30	240	49.4	.28	0.32	.31	0.44	.97
2a	1		60				.15	0.85	.98
		20	60	24.8	.28	0.10	.29	0.58	.97
		40	60				.22	0.36	.99[a]
		60	80				.18	0.82	.95[a]
		60	100				.30	0.39	.96[a]
2a	2		60				.18	1.45	.98
		20	60	21.3	.34	0.30	.32	1.96	.99
		40	60				.22	1.85	.99[a]
		60	80				.18	1.43	.97[a]
		60	100	61.0	.18	0.40	.31	1.52	.98
2a	3		60				.19	3.62	.99
		20	60	21.5	.24	1.21	.31	1.52	.98
		40	60	40.9	.19	1.08	.22	2.39	.99
		60	80	57.0	.14	1.16	.26	2.88	.99
		60	100	65.6	.28	1.13	.16	1.14	.99
2a	4		60				.26	0.73	.99
		20	60	19.9	.41	0.51	.43	0.69	.92
		40	60	33.4	.22	0.40	.33	0.80	.99
		60	80	47.4	.16	0.27	.31	0.86	.99
		60	100	54.2	.27	0.34	.30	0.60	.99
2b	5		120				.16	0.94	.99
		40	120	55.5	.41	0.11	.28	0.47	.99
		80	120	89.4	.21	0.79	.11	1.23	.99
		120	160				.23	1.57	.99[a]
		120	200	124.8	.27	0.22	.24	0.90	.99
2b	6		120				.18	1.16	.99
		40	120	41.7	.42	0.37	.38	0.92	.98
		80	120	78.2	.17	0.40	.28	1.32	.99
		120	160				.26	1.32	.98[a]
		120	200	125.5	.21	0.19	.31	1.11	.99

Appendix (*continued*)

Experiment	Rat	FI S	FI L	P S	cv S	h S	cv L	h L	r^2
2b	7		120				.22	1.01	.99
		40	120	43.2	.28	0.79	.49	0.77	.90
		80	120	80.5	.20	1.25	.20	1.22	.90
		120	160				.33	1.46	.91[a]
		120	200	119.7	.28	0.69	.22	0.95	.99
2b	8		120				.23	0.78	.99
		40	120	39.5	.43	0.20	.34	0.77	.99
		80	120	75.8	.19	0.52	.23	1.27	.99
		120	160	111.7	.13	0.30	.25	1.11	.99
		120	200	139.6	.30	0.37	.15	0.33	.99
3a	23		30				.13	0.33	.97
		30	45				.26	0.87	.98[a]
		30	60	32.5	.17	0.41	.21	0.73	.98
		30	120	34.8	.16	0.53	.19	0.53	.95
		30	240	36.3	.29	0.44	.44	0.23	.96
3a	24		30				.17	0.93	.97
		30	45	32.0	.22	0.69	.30	2.26	.99
		30	60	32.4	.17	2.03	.18	1.98	.98
		30	120	34.0	.22	1.81	.22	1.15	.97
		30	240	31.9	.23	2.87	.28	1.27	.97
3a	25		30				.24	1.39	.99
		30	45				.26	0.81	.99[a]
		30	60	31.9	.26	0.51	.25	0.91	.99
		30	120	31.5	.27	1.04	.24	0.92	.98
		30	240	33.9	.27	0.51	.29	0.46	.99
3a	26		30				.23	0.62	.91
		30	45				.27	1.21	.99[a]
		30	60	29.7	.24	1.04	.31	1.31	.99
		30	120	36.4	.15	0.84	.17	0.80	.98
		30	240	30.2	.39	0.92	.65	0.11	.98
3b	33	15	300	21.8	.40	0.61	.22	0.39	.98
		30	300	36.4	.32	0.51	.33	0.18	.98
		45	300	48.3	.29	0.94	.22	0.61	.98
		60	300	65.6	.30	0.78	.26	0.37	.98
		75	300	77.5	.28	0.54	.43	0.39	.98
3b	34	15	300	20.0	.54	0.60	.21	0.62	.96
		30	300	33.7	.49	0.34	.47	0.16	.90
		45	300	45.6	.36	1.00	.23	0.73	.96
		60	300	60.6	.36	0.60	.36	0.33	.95
		75	300	75.5	.42	0.33	.38	0.37	.99
3b	35	15	300	21.4	.56	0.61	.24	0.45	.99
		30	300	30.6	.41	0.53	.63	0.17	.95
		45	300	52.0	.33	0.79	.35	0.56	.96
		60	300	64.7	.35	0.67	.33	0.40	.98
		75	300	81.1	.37	0.39	.50	0.46	.90
3b	36	15	300	48.5	.44	0.09	.18	0.67	.99
		30	300	38.5	.32	0.41	.22	0.26	.98
		45	300	59.8	.23	0.62	.17	0.92	.99
		60	300	73.4	.20	0.74	.17	0.68	.99
		75	300	92.2	.21	0.72	.13	0.68	.99

Note. Single fixed-interval (FI) values are given as FI L only. FI S and FI L = shorter and longer FI value in mixed-FI schedule (in seconds), respectively; P S = peak location, in seconds, of fitted Gaussian curve corresponding to FI S; cv S and cv L = coefficients of variation of fitted shorter and longer curves, respectively; h S and h L = peak heights (responses/second) of fitted shorter and longer curves, respectively; r^2 = proportion of variance accounted for by the curve fit.

[a] No two-peak fit was possible.

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