DURATION COMPARISON: RELATIVE STIMULUS DIFFERENCES, STIMULUS AGE, AND STIMULUS PREDICTIVENESS

D. Alan Stubbs, Leon R. Dreyfus, J. Gregor Fetterman, David M. Boynton, Noreen Locklin, and Laurence D. Smith

UNIVERSITY OF MAINE, VASSAR COLLEGE, AND INDIANA UNIVERSITY-PURDUE UNIVERSITY AT INDIANAPOLIS

Under a psychophysical trials procedure, pigeons were presented with a red light of one duration followed by a green light of a second duration. Eight geometrically spaced base durations were paired with one of four shorter and four longer durations as the alternate member of a duration pair, with different pairs randomly intermixed. One choice was reinforced if red had lasted longer than green, and a second choice was reinforced if green had lasted longer. Performance was compared when all the base durations and their pair members were included (entire-range condition) or when only the four longest base durations and their comparison durations (restricted-range condition), supporting a memory-based account. Sensitivity was lower under the restricted-range condition. Under both conditions, a bias to report "green as longer" increased as the second green duration increased. Bias changed as a matching function of the green-duration predictiveness of the correct choice. The results are related to a quantitative model of timing and remembering proposed by Staddon.

Key words: timing, time perception, memory, duration comparison signal detection, matching, relational learning, key peck, pigeons

Perception, cognition, and learning all converge on the problem of timing, and the study of timing has become more central in each of these areas over the past quarter century. Traditionally, research and theories about timing in humans have been categorized under the label of time perception (Woodrow, 1951). Many studies, both with humans and other species, have employed psychophysical procedures (Allan & Kristofferson, 1974; Gibbon & Allan, 1984; Michon & Jackson, 1985). Due to increased interest, the topic is now considered in separate chapters in basic texts on perception (e.g., Coren & Ward, 1989; Schiffman, 1990). Issues concerning the spacing of events over time are of obvious importance for the study of cognition (e.g., McCabe & Balzano, 1986), and much of the recent research and theorizing about human time experience have come from information-processing views and cognitive-attentional views (e.g., Block, 1990; Macar, Pouthas, & Friedman, 1992). Increasing attention to timing by nonhuman animals owes a great deal to the information-processing internal-clock theory and related research of Gibbon, Church, and their colleagues (Church, 1984; Gibbon, 1991; Gibbon & Church, 1990). In the area of learning, the relation between behavior and temporal spacing of relevant events has long been studied (Richelle & Lejeune, 1980). But, in the past 15 years, the number of research papers, quantitative accounts, and theories has risen dramatically (Church & Broadbent, 1991; Gibbon, 1977; Killeen, 1991; Killeen & Fetterman, 1988; Stephens & Krebs, 1986). The present experiments draw from these areas and provide information about each.

Studies of animal time perception can be categorized into two broad procedural categories: procedures based on temporally defined schedules of reinforcement, and procedures based on more perceptual, psychophysical methods. Schedule-based procedures include fixed-interval (FI) and differential-reinforcement-of-low-rate (DRL) schedules. Under FI schedules, food is scheduled for the first response after an interval of time has elapsed, and animals on these schedules respond at a higher rate as the time to food approaches.

We thank John Staddon for his informative comments on an earlier paper (Dreyfus, Fetterman, Smith, & Stubbs, 1988) that contributed to several of the manipulations we report; in his comments, he suggested a theory of timing and remembering that we develop in this paper. The research was supported in part by grants to J.G.F. from the National Science Foundation (BNS-9021562) and NIMH (RO1 MH 48359). Correspondence should be addressed to D.A.S. or L.D.S., Psychology Department, 5742 Little Hall, University of Maine, Orono, Maine 04469-5742; to L.R.D., Department of Psychology, Vassar College, Poughkeepsie, New York 12601; or to J.G.F., Department of Psychology, LD 3124, 402 Blackford Street, Indianapolis, Indiana 46202-3272.

Under DRL schedules, animals gain reward by spacing their responses by a minimum amount of time. Under psychophysical procedures, an animal might be trained to emit one response if a stimulus lasts less than 10 s and another if the stimulus lasts longer. Psychophysical procedures offer several advantages over schedule-based procedures. Analyses of factors affecting sensitivity and biasbasic aspects of signal detection theory (Macmillan & Creelman, 1991)—are possible; the procedures and analyses can be related to the long-standing procedures and results of human psychophysics; comparisons across procedures and experiments can be made in terms of Weber fractions; and the results are often easier to interpret than those based on ratebased scheduling procedures.

The present research is psychophysical in nature and is an extension of our prior work on a duration-comparison task (Dreyfus, Fetterman, Smith, & Stubbs, 1988; Fetterman & Dreyfus, 1986, 1987; Stubbs, Dreyfus, & Fetterman, 1984). Under the basic task, pigeons were shown a red light of one duration followed by a green light of a second duration, and were required to make one choice if red had lasted longer and a second choice if green had lasted longer. Many duration pairs were intermixed, producing a task that was psychophysical in nature with a graded mix of pairs differing by lesser or greater amounts of time. The task is fundamentally different than those in other procedures used to study timing in animals. In these other tasks, performance is assessed with respect to a constant criterion time. Response rates are measured at different times in an FI schedule when food is delivered for the first response after 60 s; under a psychophysical task, animals may be trained to emit one response if a light lasted less than a criterion of 10 s and second response if the light lasted longer. In contrast, the durationcomparison procedure provides a task in which the animal responds to ever-changing duration pairs across trials. As such, the procedure is a relational learning task involving temporal stimuli.

The basic findings are that pigeons readily learn the discrimination and that discriminability is a function of the relative difference between the two durations. These findings agree with those of other psychophysical procedures (e.g., Gibbon, 1977; Stubbs, 1979), and demonstrate that discriminability depends on the relative difference of the duration pair members, in accord with Weber's law. These results hold under the basic duration task (e.g., Dreyfus et al., 1988). They also hold under a ratio-comparison variation (e.g., when birds were trained to report whether the duration of green was twice as long as red or four times shorter) (Fetterman, Dreyfus, & Stubbs, 1989). Finally, similar results were observed when different choices were reinforced depending on which color pair was longer in a sequence of four durations: red-green-red-green (a temporal integration task; Stubbs et al., 1984).

The present experiment was conducted to address questions raised by our previous work and to provide new information not covered in the prior reports. One set of questions concerns the memory aspects of the procedure. The sequential presentation of the durations produced a delay between the first duration and the choice that was imposed by the second duration. A delay between a stimulus and a choice implies lower choice accuracy according to most accounts of memory. The implication is that discrimination performance will be lower in the duration-comparison task when longer values of the second duration (and hence longer delays between the first duration and choice) are presented. Some of our findings agree with this general interpretation (Dreyfus et al., 1988). In one experiment, different duration ranges were employed (0.5 to 16 s, 1 to 32 s, 2 to 64 s, and 4 to 128 s); discrimination accuracy decreased as duration range increased, and also decreased as the average delay between the first duration and choice increased. However, when we considered performance within a particular range, accuracy measures appeared to be similar whether the duration pair was relatively short (e.g., 1 s red followed by 2 s green) or long (10 s vs. 20 s). If memory for the first duration is increasingly degraded by longer second durations, it seems that accuracy should decline both within and across ranges. Unfortunately, the procedure for generating durations made precise comparisons difficult within a range of duration pairs. Durations were produced probabilistically, providing several hundred different pairs but with the disadvantage that there were too few instances of each pair to permit specific comparisons (e.g., shorter and longer pairs with a 2:1 ratio of red to green). Instead, analyses relied on approximations by placing different pairs in categories (e.g., instances in which red was two to four times longer than green were grouped together). Thus it was possible to provide general answers to a number of questions, but the data did not permit the more ideal, specific comparisons. In the present experiments, duration pairs were arranged differently, with one goal being a more exact specification of the stimuli so that precise comparisons could be made about sensitivity and bias. The more explicit control of duration pairs affords a more definitive answer to questions raised by our earlier research and allows us to relate the findings to a theory of timing and remembering (Staddon, 1983, 1984).

METHOD

Subjects

Six White Carneau pigeons, maintained at 85% of their free-feeding weights, served as subjects. They were fed after experimental sessions as necessary to maintain weights, and were given unlimited access to water and grit in their home cages. Three pigeons were experimentally naive; 3 had experience on a concurrent-schedules choice procedure and, just prior to the present experiment, training on response-comparison and duration-comparison tasks that shared many features with the present task.

Apparatus

Experimental sessions were conducted in three sound-insulated, ventilated three-key pigeon chambers of the ice-chest variety (cf. Ferster & Skinner, 1957). Specific details of chamber design and dimensions can be found in Fetterman and Stubbs (1982). Sessions were arranged and data recorded by Apple II[®] computers that were connected to the chambers by MED Associates[®] interfaces.

Procedure

General procedure. Sessions were conducted 7 days a week. Choice responses were reinforced depending on which of two durations was longer under a psychophysical trials procedure. For each trial, the center key was lit by red light for the first of two durations and then green for the second duration, with both events scheduled independently of behavior and with different durations on each trial. The houselight was on and the side keylights off during both durations. The green light ended after a duration either shorter or longer than that of red, and then the two side keys were lit, one by red light and the other by green. The position of red and green choice keys alternated irregularly over trials, with each presented equally on the left and right over the course of a session. A red side-key response was "correct" if the duration of red had been longer than that of green. A green side-key response was "correct" if green had lasted longer than red. Correct choices intermittently produced 2-s access to food (details of food scheduling are given below); when food was delivered, the feeder light was illuminated and all keylights and the houselight were turned off. A 10-s blackout, during which all lights were off, followed food and all other correct and incorrect choice responses. A new trial followed the blackout.

Duration pairs. Eight durations were treated as "base" durations: 2.0, 2.8, 4.0, 5.6, 8.0, 11, 16, and 22 s. Each was paired with "comparison" durations of the alternate color, producing approximate ratios (comparison duration : base duration) of 0.25, 0.35, 0.50, 0.70, 1.4, 2.0, 2.8, and 4.0. Table 1 shows the base durations and the comparison durations paired with each. The geometric series of base durations as well as the related geometric series of comparison durations were selected to honor another area that focuses on time and was done in commemoration of the recent 150th anniversary of the birth (or, more specifically, public announcement) of photography (Newhall, 1982; Szarkowski, 1989). Readers may recognize the sequence as the f-stop aperture settings on cameras. The series is approximate, because we used the values written on cameras rather than the more precise values in the series (e.g., 11.2 is twice 5.6, and 22.4 is four times longer). Pigeons, or for that matter people, cannot discriminate such fine differences, so the approximation was used. When, for example, the base duration was 8 s, it was paired with shorter durations of 2, 2.8, 4, and 5.6 s, and with longer durations of 11, 16, 22, and 32 s. The table shows 64 pairs. However, the duration pairs were arranged with both red (first duration) and green (second duration) treated as the base duration, producing

Table 1

Base durations (BD) and the comparison durations (CD) paired with each, with duration ratios (CD/BD) given at the top (see text for details). On half the trials, green durations were arranged as based durations with red as comparisons; on the other half, red durations were arranged as base durations.

0.25	0.35	0.5	0.75	BD	1.4	2	2.8	4
0.5	0.7	1	1.4	2	2.8	4	5.6	8
0.7	1	1.4	2	2.8	4	5.6	8	11
1	1.4	2	2.8	4	5.6	8	11	16
1.4	2	2.8	4	5.6	8	11	16	22
2	2.8	4	5.6	8	11	16	22	32
2.8	4	5.6	8	11	16	22	32	45
4	5.6	8	11	16	22	32	45	64
5.6	8	11	16	22	32	45	64	90

a total of 128 pairs. In addition, the set of problems was repeated each session with red and green stimuli in the choice phase on different side keys, providing a total of 256 trials. The computer program provided a different order for these 256 problems each session. Within the 256 trials, there were 84 unique duration pairs (e.g., 2 s of red followed by 8 s of green was considered as a unique pair, but this pair was arranged both with red and green as the base duration and with red and green on different side keys during the choice phase).

The task was arranged as a relational discrimination, yet use of any finite set of duration pairs means that some durations could be predictive of the correct choice by themselves. Choice responses could therefore be influenced by the *relational* aspects of the task (the intended duration ratios) or by the absolute duration of one stimulus if it was predictive of the correct choice (Dreyfus, 1992; Dreyfus, Fetterman, Stubbs, & Montello, 1992). Table 1 indicates, for example, that a 90-s duration of red or green was always paired with a shorter duration of the alternate color. Duration pairs were constructed so that the specific duration of red or green could not easily predict choice. In the middle range of durations, green durations were paired with red durations that were equally likely to be shorter or longer. At the extremes, however, one duration was paired with shorter or longer durations in a more predictable way. When, for example, green was in the range of 0.5 to 1.4 s, it was always shorter than its red pair member. When green was 2 s, including instances in which green was the base duration and those in which it was the comparison, there were eight instances in each session when green was longer than red and 16 instances when red was longer (i.e., green was longer on one third of the trials). For green base durations from 2 s to 22 s, the probabilities of green being longer than red were .33, .38, .43, .47, .53, .57, .62, and .67, respectively. Thus, the predictiveness of green alone, or for that matter red alone, depended on the specific base duration. At the extreme values, the absolute duration of a stimulus was predictive of the correct choice; at middle values, absolute duration was not predictive.

Experimental conditions. The 3 naive pigeons were trained to peck on the center key by the method of successive approximation, and then were exposed over five sessions to conditions that gradually approximated the duration-comparison task. Training proper began with 50 sessions with both choice keys lit and 128 trials per session, with food delivered for each correct choice. Then, the pigeons were exposed to 40 sessions with 256 trials each session and intermittent reinforcement for correct responses. Each reinforcer was assigned for a correct red-key or for a correct green-key response. Blackouts resulted unless a correct choice was made to the designated key. If, for example, a reinforcer was assigned for a correct green-key response, correct redkey choices would not yield food. This procedure provided reinforcement for approximately 50% of the correct choices and ensured control over relative reinforcement rate for selecting red and green stimuli as longer (Stubbs, 1976).

Prior to the present experiment, the 3 experienced pigeons had been trained on response-comparison tasks (pecks to red and green choice keys were reinforced depending on whether more pecks had been emitted on a red or a green key) and duration-comparison tasks that were the same as in the present task except for the specific durations presented. Given the prior exposure to similar procedures, these pigeons were exposed for 50 sessions to the same conditions that the naive birds received for their final 40 sessions: 256 trials each session, base durations from 2 to 22 s, and intermittent reinforcement.

Following the first condition (entire-range

condition), all pigeons were transferred to a restricted-range condition in which only the four longest base durations were presented (8, 11, 16, and 22 s) along with their comparison durations (see Table 1, bottom four rows). Given red and green as base durations and the two red-green choice-key arrangements, 128 trials were presented each session. Reinforcers were arranged intermittently as in the first condition. This restricted-range condition was in effect for 20 sessions.

After these two conditions, the 3 originally naive pigeons were reexposed to the entirerange condition for 30 sessions and then the restricted-range condition for 19 sessions, to assess whether performance would be similar across two determinations.

RESULTS

Figure 1 shows probability of a green-key response (response of green as longer than red) as a function of the green/red duration ratio computed for the final 30 sessions of training on the entire-range condition and the 20 sessions of the restricted-range condition. The group data as well as those for individual pigeons indicate that the probability measure increased as an ogival function of increasing duration ratio under both conditions. Figure 1 also indicates a difference in performance between conditions, with the function being less steep under the restricted-range condition. To compare the curves, we transformed the probability scores to z scores to straighten the functions (Guilford, 1954) and calculated slopes for each pigeon for the two conditions. The results of a two-tailed, paired t test confirm the visual representation: Slopes were significantly higher under the entire-range condition, t(5) = 4.28, p < .01.

Inspection of the ogives reveals a possible asymmetry in the functions, a difference that relates to whether green or red was the longer pair member. The pigeons were less accurate for comparable ratios (e.g., a 4:1 ratio of longer to shorter duration) when green (second duration) was longer as opposed to when red (first duration) was longer. Accordingly, we took the probability data for both conditions and calculated accuracy measures for each duration ratio. The group data for the entirerange condition make the point. As the ratio of longer to shorter duration changed from 4:1 to 1.4:1, accuracy measures with red as longer and green as longer were, respectively, 81% and 79% (4:1), 80% and 75% (2.8:1), 72% and 67% (2:1), and 63% and 59% (1.4:1). Thus, accuracy decreased as the duration ratio approached 1:1, and small but consistent differences revealed higher accuracy when red was the longer pair member across pigeons and conditions. A three-way repeated measures ANOVA compared accuracy for the two duration ranges, compared accuracy as duration ratios changed, and compared accuracy for the comparable ratios with red and green as the longer member (e.g., red as four times green vs. green as four times red). The important finding for present purposes is that accuracy was, in fact, statistically significantly higher when red was longer than for comparable cases when green was longer, F(1, 5) = 15.2, p < 15.2.02. The other differences confirm what Figure 1 and the prior analysis show. There was a statistically significant effect for duration range, F(1, 5) = 20.8, p < .007: Accuracy was lower under the restricted range. The effect for duration ratio was also statistically significant, F(3, 15) = 69.6, p < .001, demonstrating a decrease in accuracy as duration ratios approached 1:1.

The ogives display performance when all duration pairs were included. Ideally, performance should be compared for each of the eight base durations and their associated durations. However, comparisons involving eight ogives would be cumbersome and figures presenting them hard to interpret. Accordingly, Figure 2 uses summary measures of sensitivity (A')across the eight categories of green durations from 2 to 22 s, where each duration was paired with four shorter and four longer red durations.¹ The A' measure is a nonparametric measure of sensitivity that is appropriate when several stimulus values are used and assumptions about normal distributions of "signal" and "noise" are violated. This measure was

¹ This analysis and those that follow are computed with respect to the second duration. Similar analyses can be computed with respect to the first duration. However, Dreyfus et al. (1992) have reported both and have demonstrated that the second duration exerts greater influence. Such an effect agrees with other research concluding that the more recent events in a series have greater effects (e.g., Alsop & Honig, 1991; Shimp, 1976).

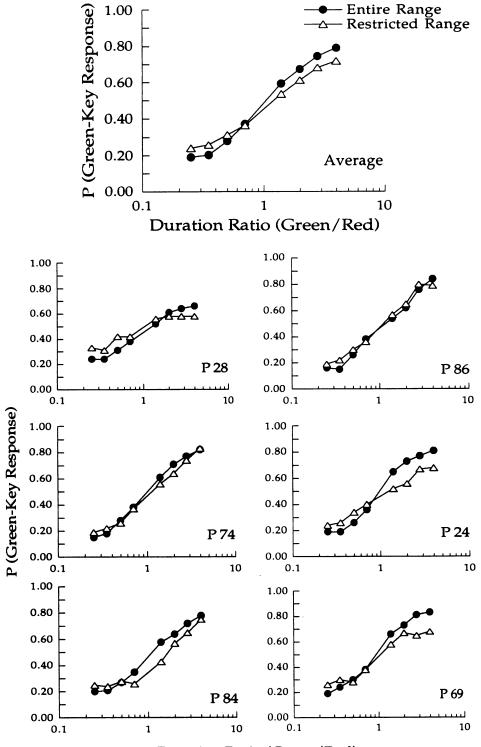




Fig. 1. Probability of a green-key response as a function of duration ratio (green duration : red duration) totaled over the last 30 sessions of the entire-range condition and the 20 sessions of the restricted-range condition. Duration ratios are presented on a logarithmic axis. The top panel shows data averaged for 6 pigeons; the remaining panels show data for individual pigeons.

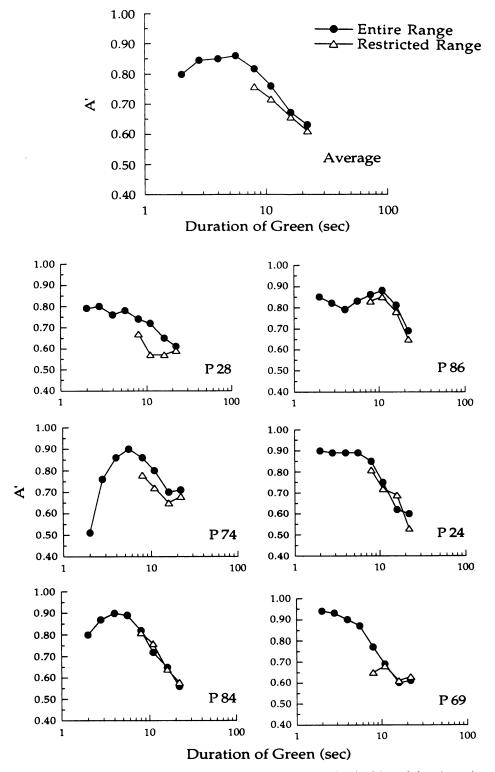


Fig. 2. Sensitivity (A') as a function of the duration of the green stimulus (and its red duration pair members) totaled over the last 30 sessions of the entire-range condition and the 20 sessions of the restricted-range condition. The green duration is presented on a logarithmic scale. The top panel shows averaged data for 6 pigeons; the remaining panels show data for individual pigeons.

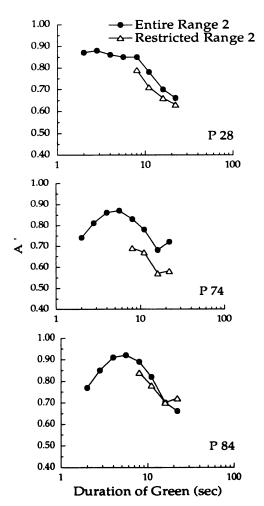


Fig. 3. Sensitivity (A') as a function of the duration of the green stimulus (and its red duration pair members) totaled over the 30 sessions of the second determination of the entire-range condition and the 19 sessions of the second determination of the restricted-range condition. The green duration is presented on a logarithmic scale.

calculated based on the formula given by Grier (1971) as follows:

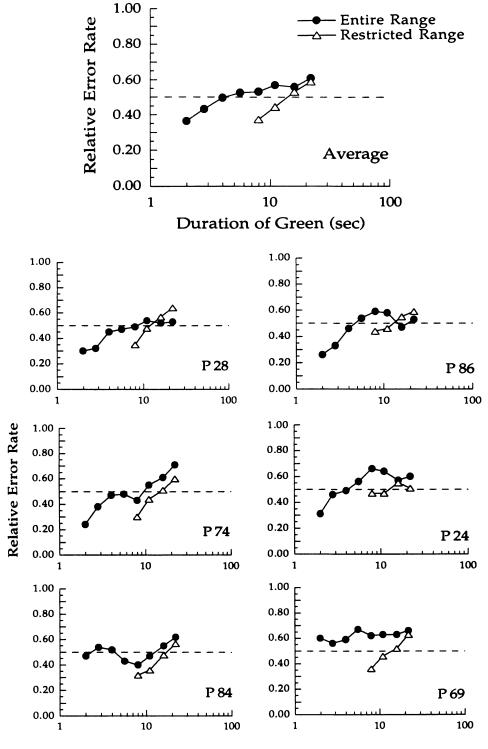
$$A' = \frac{1}{2} + \{ [p(CD) - p(FA)] \\ \cdot [1 + p(CD) - p(FA)] \} \\ \div \{ 4p(CD)[1 - p(FA)] \}.$$
(1)

Under the terminology of signal detection theory, p(CD) is the probability of a correct detection and p(FA) is the probability of a false alarm. Treating duration ratios (green:red) greater than 1 as signal (when green was longer than red) and ratios less than 1 as noise (when green was shorter), we defined a correct detection as a green-key response given that green was longer than red, and a false alarm as a green-key response given that red was longer. The A' measure correlates highly with the simpler percentage correct measure, but A'is independent of changes in accuracy that may result from different response biases. Values of A' range between .5 (insensitivity) and 1.0 (perfect discriminability).

Consider performance when the entire range of duration pairs was presented (Figure 2). The most salient feature of performance is that A' scores decreased as duration of green increased. All pigeons showed this effect. The A' scores were also lower for the shortest durations for 2 pigeons (P74 and P84), and their data lowered performance in the group panel. The remaining 4 pigeons, however, demonstrated only a decrease in sensitivity as duration increased. Under the restricted range, A'scores decreased for all pigeons. An ANOVA for the entire range indicated a statistically significant decrease in A' with increasing durations of green, F(7, 35) = 7.33, p < .0001. More specific, discriminability declined as the delay between the first, red stimulus and choice increased (the delay being imposed by the duration of the second, green stimulus).

Comparison of performance under the entire-range and restricted-range conditions (Figure 2) makes two main points. First, A'scores decreased as duration of green increased from 8 to 22 s under the restricted-range condition as well as under the entire-range condition. Second, A' scores usually were lower under the restricted-range condition for group and individual data (triangles generally were below comparable circles). An ANOVA computed for the data common to the entire-range and restricted-range conditions (base durations of 8 to 22 s) demonstrated a main effect for duration, F(3, 15) = 22.30, p < .0001, and a main effect for condition, F(1, 5) = 6.89, p< .05; the interaction was not statistically significant, F(3, 15) = 1.30.

For 3 of the pigeons, a redetermination of the entire-range and the restricted-range conditions was made to ensure that the pattern of behavior could be recaptured. Figure 3 indicates that it could. The data for P28 and P74 show that points were higher under the entirerange condition than for comparable points under the restricted-range condition in all comparisons. The data for P84 show one exception and one virtual tie. This bird also showed the greatest deviation from the general



Duration of Green (sec)

Fig. 4. Relative error rate (see text for method of calculation) as a function of the duration of the green stimulus for the last 30 sessions of the entire-range condition and the 20 sessions of the restricted-range condition. The green duration is presented on a logarithmic scale. The top panel shows averaged data for 6 pigeons; the remaining panels show data for individual pigeons.

pattern found for the 6 pigeons during the first determination (compare its performance with that in Figure 2).

Figure 4 shows that changes also occurred in response bias as duration of green lengthened under both conditions. That is, there was a shift in the proportion of errors, with relatively more errors to the red key when durations were short and more errors to the green key when durations were long. A bias measure, relative error rate (Stubbs, 1976), was computed as follows:

$$p(\mathbf{FA})/[p(\mathbf{FA}) + p(\mathbf{M})], \qquad (2)$$

where p(FA) represents, as in Equation 1, the probability of a green-key error (incorrect report of green as longer than red) when the first, red duration was longer, and p(M) represents a red-key error (red as longer) when green was actually longer. This measure compares the relative numbers of errors to the green as opposed to the red side key. Values above .5 indicate a bias to respond green (and report the duration of green as longer), and values below .5 indicate a bias to respond red. The filled circles in Figure 4, which present data across eight categories under the entirerange condition, show that relative error rates generally increased as green duration increased. An ANOVA calculated on relative error rates for this condition revealed a statistically significant change as the duration of green increased, F(7, 35) = 7.46, p < .0001. Comparison of performance under the restricted-range condition with that of the entire range indicates that the relative number of green-key errors increased under both conditions as green duration increased. The slopes of the functions differed, however, for the two conditions. Figure 4 suggests a greater change in relative error rates under the restricted-range condition as the duration of green increased from 8 to 22 s. A two-way (Duration \times Condition) ANOVA demonstrated a significant main effect for duration, F(3, 15) = 9.15, p <.001, a main effect for condition, F(1, 5) =14.97, p < .01, and a significant interaction, F(3, 15) = 10.29, p < .01. These findings indicate that relative error rates increased over both conditions, and more so under the restricted range, resulting in convergence of the functions as the duration of green approached 22 s. This same pattern of change under the two conditions was observed for the redetermination of entire-range and restricted-range conditions for 3 subjects.

The different patterns in bias in the different conditions can be related to differences in the predictiveness of the green duration in the two conditions. Given the eight categories of green in the original task, the probability that green was longer than red changed from .33 to .67 over the eight categories, and from .53 to .67 over the four longest categories (see Duration Pairs section of the Method). When, however, only the four longest base durations were used for the restricted-range condition, the probabilities that green was longer than red were .36, .45, .55, and .64 as the duration category increased from 8 s to 22 s. If animals are responsive to probability of occurrence of food as absolute durations vary, the greater change in predictiveness of green over these four durations could produce greater change in relative error rates. Accordingly, the data from Figure 4 are presented again in Figure 5 as a function of the probability of green being the longer of the two durations. The resulting plot is a "matching" figure common to operant choice research (e.g., Davison & McCarthy, 1988) and applicable as well to bias in temporal discriminations (e.g., Stubbs, 1976, 1980). To compare performance, we expressed the relative error-rate data in terms of the generalized matching equation (Baum, 1974), which has become the standard way of describing matching data, and which formulates matching in terms of a power function relating behavior ratios and reinforcement ratios. For present purposes the relevant equation can be expressed as

$$\frac{p(\mathrm{FA})/p(\mathrm{M})}{=k[p(\mathrm{G} > \mathrm{R})/p(\mathrm{G} < \mathrm{R})]^n}, \qquad (3)$$

where p(FA)/p(M) converts the behavior measure to a ratio of green-key divided by redkey errors, p(G > R) and p(G < R) are the probabilities that green is longer and shorter than red, respectively, for a particular duration of green, and k and n are constants. Taking the logarithm of both sides of the equation produces a linear relation, with n representing the slope of the function.

Figure 5 demonstrates that bias increased in a similar way across conditions as the probability of green being the longer pair member increased. Straight lines were fit to the data by means of linear regression. Table 2 gives

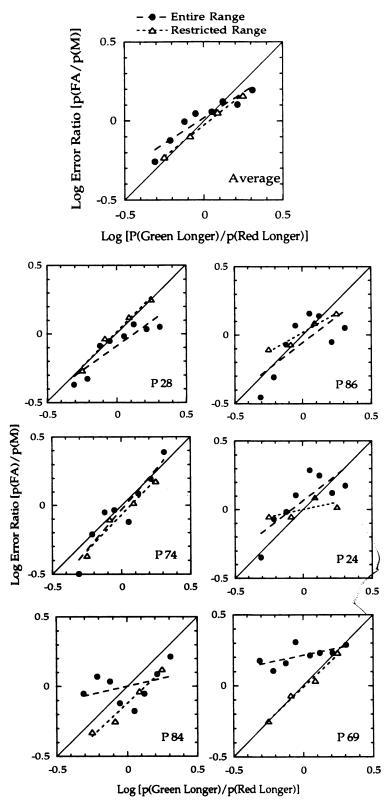


Fig. 5. Relative error ratio as a function of the relative ratio of the green duration being longer than red for different duration pairs when data were grouped according to the duration of green (and associated red-duration pairs). Data are totaled across the last 30 sessions of the entire-range condition and the 20 sessions of the restricted-range condition. The top panel shows averaged data for 6 pigeons; the remaining panels show data for individual pigeons.

Table 2

Slope, y intercept, and amount of variance (r^2) for entire range and restricted range.

Pigeon	Range	Slope	y intercept	r^2
Average	entire	0.65	0.01	.88
0	restricted	0.80	-0.02	.99
P28	entire	0.72	-0.09	.81
	restricted	1.03	0.02	.98
P74	entire	1.18	-0.03	.88
	restricted	1.05	-0.07	.97
P84	entire	0.02	0	.15
	restricted	0.94	-0.12	.98
P8 6	entire	0.76	-0.06	.55
	restricted	0.57	0.02	.95
P24	entire	0.77	0.06	.64
	restricted	0.21	0	.46
P69	entire	0.21	0.21	.44
	restricted	0.93	-0.01	.98

information on slope, y intercept, and amount of variance accounted for. Figure 5 and Table 2 indicate that exponents were below 1.0 in nine cases, a finding of undermatching. The results of a paired t test demonstrated that the slopes were not significantly different statistically, t(5) = -0.76, for the two conditions. Thus, the differences in Figure 4 vanish when one considers them from a different perspective, by taking relative predictiveness into account. The graphical and statistical findings demonstrate that response bias varied as a function of relative predictiveness in a similar way, regardless of condition.

DISCUSSION

The results have demonstrated four related main findings that we first sketch and then cover in turn. First, discriminability decreased as the duration of the second, green stimulus increased, providing a longer delay between the first duration and choice. This finding alters the conclusions of our prior work (Dreyfus et al., 1988; Fetterman et al., 1989). These findings are in accord with a theory of timing and remembering developed by Staddon (1983, 1984), and the link will be developed below. Second, discriminability was lower under the restricted-range condition compared to the entire-range condition. This finding sheds new light on the explanation of Dreyfus et al. (1988). Third, many of the comparisons provide information about the influence of relative and absolute duration as they affected sensitivity and bias. Fourth, stimulus predictiveness affected response bias. This finding derives from signal detection theory and the matching relation.

Timing and Remembering

In prior experiments, there appeared to be no difference in accuracy for shorter or longer pairs within a range of durations (Dreyfus et al., 1988). The present results demonstrated, however, that sensitivity declined as the duration of green increased. This finding is new; it alters conclusions of our prior work, and it suggests a memory-based account. We mean nothing mysterious about memory; the term is simply descriptive of the changes in control by a prior stimulus that occur over time. Research on animal "working" memory indicates lower accuracy when a longer delay intervenes between a stimulus and choice. In the familiar delayed matching-to-sample procedure, for example, a sample is presented and a delay intervenes before comparison stimuli occasion a choice response. Accuracy of choosing the prior sample decreases with increases in the delay. Similarly, accuracy decreased as the duration of the pairs increased and the delay between the first duration and choice lengthened. A 0.5-s duration of red followed by 1 s of green provided a shorter delay than 22 s of red followed by 45 s of green, and accuracy was higher in the former case.

Why do conclusions drawn from past and present results differ? The best answer is that discriminability probably did decrease as a function of duration in past experiments, but the effect was not revealed by the procedures and analyses of those experiments. In most earlier versions (see Dreyfus et al., 1992, for one exception), durations were arranged probabilistically by pulses sent to a probability gate, a method that produced an exponential distribution of durations. Given the large number of duration pairs and the rarity of some, specific comparisons could not be made; most comparisons in our previous work grouped duration pairs into short and long categories on the basis of total duration (i.e., first plus second duration). In contrast, the present procedure was designed to provide specific comparisons of sensitivity and bias for different but comparable pairs (e.g., would there be differences when red and green were, respectively, 1 and 2 s, 2 and 4 s, 4 and 8 s, 8 and 16 s, or 16 and 32 s?). These specific comparisons revealed differences, sometimes subtle, that would be difficult to discover with prior versions of the task.

The resolution of the earlier discrepancy makes viable once again a memory account of the change in sensitivity, and several features of the data indicate that memory is involved. First, Figure 2 showed that sensitivity decreased as a function of increasing duration of the second duration. Longer durations of green produced increased delays between the first duration and choice, and led to effects like those observed in other delayed choice experiments (e.g., Roitblat, 1987; Spetch & Rusak, 1992).

Second, an analysis of the ogival data of Figure 1 revealed that accuracy was a function of relative duration difference, but also depended on whether the first or second duration was the longer duration. With a 4:1 ratio between the durations, for example, accuracy was high, but accuracy was slightly higher when red (the first duration) as opposed to green (the second duration) was four times longer. This outcome also accords with a memory account. In the present case, this memory account explains not only lower accuracy for longer duration pairs but also the asymmetry in accuracy for reciprocal duration ratios (e.g., 1:4 vs. 4:1).

A third aspect of the data—the difference in sensitivity over entire and restricted ranges shown in Figure 1—may also be viewed as a memory effect. The A' data of Figure 2 point to one reason for the difference seen in Figure 1. The ogival data were based on all duration pairs included under the respective conditions. As a result, data for the entire-range condition included problems with shorter and longer duration pairs (all eight base durations and associated pairs were included) for which discriminability was relatively high (short pairs) and low (long pairs). In contrast, the restricted-range condition included only the longer duration pairs (the four longest base durations and pair members) for which discriminability was relatively low. Differences in the ogival data appear to have resulted chiefly from inclusion of only the longer problems under the restricted range.

A Theory of Timing and Remembering

Our findings are consistent with Staddon's (1983, 1984) theory of timing and remembering, and an extension of this theory, which treats the duration-comparison case, describes many aspects of our results. A basic assumption of the theory is that the salience of an extended event declines as a function of time since that event, with the decline more rapid at first and then slower later. A recent event will be more salient than an equivalent event further in the past. Staddon's account is a temporal perspective theory that relies on an analogy with distance perception.

Staddon proposed a hyperbolic function for timing and remembering of durations in which salience (transformed age) depends on the duration of the event (longer durations are more salient than shorter durations) and the time since the event ended (durations in the distant past are less salient than durations in the notso-distant past). It takes the general form

$$A = C - D^k, \quad D^k \le C, \quad -1 < k < 0, \quad (4)$$

where A is the transformed age of the duration, D is the nominal duration (or in the present case, the time since the keylight was turned on), C is some constant (which must be greater than zero) representing the time between the end of the duration and the subject's evaluation of it, and k is a negative exponent. For the duration-comparison task, discrimination depends on a comparison of the transformed age of two events: the total trial duration (red plus green) and green alone,

$$A_{\rm td} = C - TD^{k} \quad \text{and} \quad A_{\rm gd} = C - GD^{k}, \quad (5)$$

where TD and GD refer to total (red + green) and green durations, respectively, and A_{td} and A_{gd} represent their transformed ages. A comparison of the transformed ages is expressed as

$$TRD = A_{td} - A_{gd}, \qquad (6)$$

where TRD is the transformed relative difference measure and A_{td} and A_{gd} are as specified in Equation 3. A simplification and working formula that removes the constant C is

$$TRD = GD^{*} - TD^{*}.$$
 (7)

Although the equations are expressed in terms of total and green durations, functionally the comparison involves the relative difference between red and green duration. But unlike a description involving Weber's law, which depends only on actual relative time differences, this characterization considers changes due to the relative salience and age of the durations.

The top panel of Figure 6 provides a graphical presentation of the theory, showing how

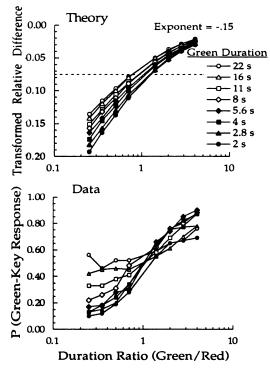


Fig. 6. The top panel shows theoretical predictions of the relation of transformed relative difference for different values of green as a function of duration ratio (see text for theoretical details). The bottom panel shows group data that relate to the theory. The bottom panel shows probability functions as duration ratio changed for the different values of green and their red-duration pairs.

transformed ("subjective") relative difference (TRD) relates to duration ratio. We selected an exponent of -0.15 and performed calculations based on the equations of the theory. Figure 6 shows TRD measures for the different duration ratios when the duration of green ranged from 2 s to 22 s. The vertical axis ranges from 0 at the top to .20. Points closer to 0 mean that green predominates (the difference between total pair duration and green duration is less); points closer to .20 mean that red predominates in the red-green pair. At the most general level then, the panel shows that the probability of a green-key response, which is related to TRD, should increase as the duration ratio increases, a finding in accord with our data. The dashed line represents an arbitrary response criterion above which the tendency is to report green as longer and below which the tendency is to report red as longer. The higher a point above the criterion line, the greater the probability of a green-key choice; the lower a point below it, the greater the probability of a red-key choice. The notion of a criterion comes from signal detection theory, and changes in hypothesized response criterion have been observed in many detection, discrimination, and recognition experiments, with both humans and nonhumans. A reason for displaying a criterion line is that predictions about choice accuracy can be made both as the duration of green increases and as the duration ratio changes.

The theory makes four predictions, two that are general and two that are more specific. First, the theory predicts a decrease in discriminability as the duration of green increases (or as duration pairs become longer). The top panel of Figure 6 shows that the functions become less steep as the duration of green increases from 2 to 22 s. As a result, the longer the duration of green, the closer, on average, are the points to the criterion line. Given that accuracy is a function of distance from the criterion line, longer pairs should be less discriminable than shorter pairs, precisely what we found. Second, the theory predicts a change in response bias as duration pairs become longer. The functions are higher as the duration of green increases. Higher functions (compare unfilled with filled symbols) predict that the birds will be more likely to report green as longer, exactly as we have found in this and other experiments (e.g., Dreyfus et al., 1988).

Third, and more specific, the functions are all negatively accelerated and less steep when green was longer, and the points are closer to the criterion line for comparable duration ratios with green as the longer stimulus than when red was longer (e.g., 4 vs. 0.25, 2.8 vs. 0.35, etc.). The theory thus suggests that accuracy might be slightly lower when green is the comparably longer pair member than when red is longer. The ANOVA calculated on the basis of this suggestion bore out this prediction of the theory, both for the entire-range and the restricted-range conditions. Fourth, the points are less widely separated for large than for small duration ratios. To assess this aspect of the theory, we calculated probability data based on the eight durations of green (and their redduration pairs). The ogival data (averaged for all 6 pigeons in the first condition) are given in the bottom panel of Figure 6. There is good agreement between theory and data. The ogives diverge more when red was longer (when the duration ratio was less than 1) and converge more when the duration of green was longer. Although the bottom panel shows group data, this pattern was also observed for individual pigeons.

The theory provides a good account of our findings. Although other memory models might also predict a lowering of discriminability for longer pairs, the predictions of Staddon's theory on bias, asymmetric accuracy, and asymmetric ogives are more specific and borne out by the results. The theory can account for other results as well, such as the choose-short effect (e.g., Spetch & Rusak, 1992) and the effects of stimulus intensity in duration-discrimination tasks (e.g., Wilkie, 1987).

Entire-Range Versus Restricted-Range Conditions

Although some aspects of the accuracy data support a memory-based explanation, there is one aspect of performance that is not covered by such an account. If the decline in performance under both restricted and entire ranges resulted only from memory limitations, then performance on identical problems under these two ranges should be comparable. Analyses of the data revealed, however, that although sensitivity decreased as a function of duration in both contexts, it was lower on individual problems under the restricted range than on those same problems under the entire range. Dreyfus et al. (1988) varied duration range and obtained related results; accuracy decreased as range increased. But this manipulation produced several correlated changes: The average trial duration increased, the overall rate of reinforcement decreased, and the absolute range of duration pairs increased. Overall reinforcement rate was ruled out as a possibility (Experiment 3 of Dreyfus et al., 1988); changes in probability of reinforcement over a wide range produced no effect on discrimination accuracy. The present findings suggest that stimulus range is not the causal factor in general because discrimination accuracy usually decreases with increases in stimulus range (e.g., Gravetter & Lockhead, 1973; Hinson & Lockhead, 1986), whereas an opposite pattern was observed here. Drevfus et al. (1988) proposed an account based on total trial duration to explain their findings, and the present findings provide more evidence for this suggestion. In the present situation, average trial duration nearly doubled with the change from the entire range to the restricted range, and discriminability differed in the two range contexts. Thus, the single invariant relation across the present and past experiments involves trial length and accuracy; accuracy decreased with increases in trial duration, and this relation did not result from correlated changes in reinforcement rate or stimulus range.

Relative Versus Absolute Stimulus Duration

Whereas the discussion to this point has focused on explanations for the way in which the second duration affected discriminability, there is another potential set of effects of absolute duration. In all versions of the durationcomparison task (e.g., Dreyfus et al., 1992), absolute duration can be predictive of the correct choice. Given duration pairs that are constituted from a finite range of stimuli, longer green durations are more often preceded by shorter red durations, and shorter green durations are more often preceded by longer red durations. Figures 3 and 4 related this feature to changes in bias, but it is also possible that this predictive aspect could influence accuracy. The question is whether and to what degree discriminability depended on relative duration differences as opposed to simply one duration of a pair. The larger issue is whether seemingly complex and intelligent behavior depends on less obvious but simpler mechanisms.

Prior findings demonstrated that both relative and absolute durations affect performance, but those earlier investigations did not determine whether the predictive aspect of absolute duration affected sensitivity as well as bias (Dreyfus, 1992; Dreyfus et al., 1988, 1992). The present results afford a better opportunity to address this question, and they provide no evidence that the predictive aspects of duration of green enhanced accuracy. This conclusion draws on two lines of evidence. First, enhancement of performance would be evidenced by an increase in A' scores when the duration of green was very short or long and therefore most predictive. The results of Figure 2 should have shown a U-shaped function had the predictive relation strongly controlled sensitivity; A' scores would have been higher at the extremes (when the green duration was most predictive) and lower in the middle (when green was least predictive). Even with the declining A' scores we observed, an effect of predictiveness of absolute duration on sensitivity could appear as an upturn at the extremes. The data provide no evidence for such an effect. In fact, discriminability was lower at the extremes for 2 or perhaps 3 pigeons (see Figure 2).

Second, we compared the rate of acquisition for different duration pairs for the 3 naive pigeons to assess whether acquisition was more rapid for problems when the predictiveness of absolute duration might augment relative duration differences (e.g., when green was very short or long and most predictive, as opposed to when green was intermediate and least predictive). There was no evidence that the predictiveness of absolute duration affected acquisition. The rate and pattern of acquisition, as measured by A', were comparable whether the duration of green was short (relatively predictive), intermediate (least predictive), or long (relatively predictive). Changes in performance due to the predictiveness of absolute duration, then, appear to be changes in response bias rather than sensitivity, and these changes take on a particular form that is in accord with the principles of signal detection theory, as we discuss below. In our prior papers, we have had to hedge whether sensitivity was influenced by relative duration differences, absolute duration, or both. The present findings allow a more definite answer: The predictiveness of absolute duration (the extent to which it predicts the correct choice) affects bias but not sensitivity.

Response Bias

The change in bias with increasing duration of the second stimulus and the greater change in bias under the restricted range relate to changes in the predictability of relative duration (and therefore the correct choice) by the second, green duration. These findings reinforce a basic point of signal detection theory about the factors affecting bias. This theory states that two factors affect response bias: (a) costs and payoffs for different choices and (b) the probability of occurrence of different stimuli (Green & Swets, 1966). Stubbs (1976), for instance, varied relative reinforcement rates for choices in a duration-discrimination task and observed a matching relation between relative error rate and relative reinforcement rate (see also McCarthy & Davison, 1979). Hob-

son (1978) varied relative reinforcement rate in a numerosity task in which one choice was reinforced intermittently if a smaller number of responses had been emitted and a second choice was reinforced if a larger number had been emitted. Of particular importance for present purposes, Hobson varied relative reinforcement rates within sessions and presented different lights that signaled relative reinforcement rate for a particular choice. These signaled changes affected response bias but not sensitivity. The implication of Hobson's work for the present experiment is clear. Green durations, in addition to their other functions in the present situation, can be viewed as acting like Hobson's lights in providing information about which response was more likely to provide food. If the differences in bias across conditions resulted from differences in the predictiveness of the green duration for the correct choice, then there should be an orderly relation between relative error rates and the relative predictiveness of green, just as orderly relations have been observed between relative response rates and relative reinforcement rates under concurrent schedules (e.g., Davison & McCarthy, 1988) and between relative error rates and relative reinforcement rates under other signal detection procedures (e.g., Stubbs, 1976). The data in Figure 5 demonstrated that response bias did in fact change as a function of relative predictiveness. This outcome places the results in the signal detection context and permits more precise statements about the influence of predictiveness of green on response bias than those warranted by prior data.

Figure 5 emphasized probability of green as a predictor of food and is consistent with the general point of signal detection theory that stimulus probability affects bias. However, reinforcement rate covaried with probability in our experiment, so the analysis does not rule out alterations in relative reinforcement rate as the more important factor. In fact, Mc-Carthy and Davison (1979) have manipulated reinforcement and probability separately and have made the case that relative reinforcement is the controlling factor affecting bias.

Conclusion

Our findings interrelate by demonstrating that stimulus durations, whether singly or in combination, had multiple functions on behavior. Discrimination accuracy depended on the relative difference between the first and second durations. But in addition, the second duration acted as a temporal buffer between the first duration and choice, and in this role affected memory for prior red durations, lowering accuracy when green was long. The particular durations comprising a duration range affected the discrimination context by altering the average trial time. Average trial time was almost twice as long under the restricted range as opposed to the entire range, and this difference also affected accuracy (e.g., Zeiler, 1991). Finally the green duration, by virtue of its proximity to choice and coupled with the information it provided about choices, acted to influence bias. The green duration provided information about relative payoffs for red-key and green-key choices, and in this role influenced response bias in an orderly way. These findings relate to a recent demonstration by Fetterman (1993) that discrimination of numerosity is controlled by both time and number (see also Fetterman et al., 1989). These conclusions underscore the point that with complex stimulus arrangements, like those used in much current nonhuman animal research, multiple aspects of complex stimuli affect behavior and complex stimuli exert multiple effects on behavior.

REFERENCES

- Alan, L. G., & Kristofferson, A. B. (1974). Psychophysical theories of duration discrimination. *Perception* and Psychophysics, 16, 26-34.
- Alsop, B., & Honig, W. K. (1991). Sequential stimuli and relative numerosity discrimination in pigeons. Journal of Experimental Psychology: Animal Behavior Processes, 17, 386-395.
- Baum, W. M. (1974). On two types of deviation from the matching law: Bias and undermatching. Journal of the Experimental Analysis of Behavior, 22, 231-242.
- Block, R. A. (Ed.). (1990). Cognitive models of psychological time. Hillsdale, NJ: Erlbaum.
- Church, R. M. (1984). Properties of the internal clock. In J. Gibbon & L. Allan (Eds.), Annals of the New York Academy of Sciences: Vol. 423. Timing and time perception (pp. 566-582). New York: New York Academy of Sciences.
- Church, R. M., & Broadbent, H. A. (1991). Alternative representations of time, number and rate. *Cognition*, 37, 55-81.
- Coren, S., & Ward, L. M. (1989). Sensation and perception (3rd ed.). New York: Harcourt Brace Jovanovitch.
- Davison, M., & McCarthy, D. (1988). The matching law: A research review. Hillsdale, NJ: Erlbaum.

- Dreyfus, L. R. (1992). Absolute and relational control in a temporal comparison task. In W. K. Honig & J. G. Fetterman (Eds.), Cognitive aspects of stimulus control (pp. 21-46). Hillsdale, NJ: Erlbaum.
- Dreyfus, L. R., Fetterman, J. G., Smith, L. D., & Stubbs, D. A. (1988). Discrimination of temporal relations by pigeons. Journal of Experimental Psychology: Animal Behavior Processes, 14, 349-367.
- Dreyfus, L. R., Fetterman, J. G., Stubbs, D. A., & Montello, S. (1992). On discriminating temporal relations: Is it relational? *Animal Learning & Behavior*, 20, 135-145.
- Ferster, C. B., & Skinner, B. F. (1957). Schedules of reinforcement. New York: Appleton-Century-Crofts.
- Fetterman, J. G. (1993). Numerosity discrimination: Both time and number matter. *Journal of Experimental Psychology: Animal Behavior Processes*, 19, 80-94.
- Fetterman, J. G., & Dreyfus, L. R. (1986). Pair comparison of durations. *Behavioural Processes*, 12, 111-123.
- Fetterman, J. G., & Dreyfus, L. R. (1987). Duration comparison and the perception of time. In M. L. Commons, J. E. Mazur, J. A. Nevin, & H. Rachlin (Eds.), Quantitative analyses of behavior: Vol. 5. The effects of delay and of intervening events on reinforcement value (pp. 3-27). Hillsdale, NJ: Erlbaum.
- Fetterman, J. G., Dreyfus, L. R., & Stubbs, D. A. (1989). Discrimination of duration ratios. Journal of Experimental Psychology: Animal Behavior Processes, 15, 253-263.
- Fetterman, J. G., & Stubbs, D. A. (1982). Matching, maximizing and the behavioral unit: Concurrent reinforcement of response sequences. Journal of the Experimental Analysis of Behavior, 37, 97-114.
- Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. Psychological Review, 84, 279-325.
- Gibbon, J. (1991). Origins of scalar timing. Learning and Motivation, 22, 3-28.
- Gibbon, J., & Allan, L. (Eds.). (1984). Annals of the New York Academy of Sciences: Vol. 423. Timing and time perception. New York: New York Academy of Sciences.
- Gibbon, J., & Church, R. M. (1990). Representation of time. Cognition, 37, 23-54.
- Gravetter, F., & Lockhead, G. R. (1973). Criterial range as a frame of reference for stimulus judgment. *Psychological Review*, 80, 203-216.
- Green, D. M., & Swets, J. A. (1966). Signal detection theory and psychophysics. New York: Wiley.
- Grier, J. B. (1971). Nonparametric indices for sensitivity and bias: Computing formulas. *Psychological Bulletin*, 75, 424-429.
- Guilford, J. P. (1954). Psychometric methods. New York: McGraw-Hill.
- Hinson, J. M., & Lockhead, G. R. (1986). Range effects in successive discrimination. Journal of Experimental Psychology: Animal Behavior Processes, 12, 270-276.
- Hobson, S. L. (1978). Discriminability of fixed-ratio schedules for pigeons: Effects of payoff value. *Journal* of the Experimental Analysis of Behavior, 30, 69-81.
- Killeen, P. R. (1991). Behavior's time. In G. Bower (Ed.), The psychology of learning and motivation (Vol. 27, pp. 295-334). New York: Academic Press.
- Killeen, P. R., & Fetterman, J. G. (1988). A behavioral theory of timing. Psychological Review, 95, 274-295.

- Macar, F., Pouthas, V., & Friedman, W. J. (Eds.). (1992). Time, action and cognition. Dordrecht: Kluwer Academic Publishers.
- Macmillan, N. A., & Creelman, C. D. (1991). Detection theory: A user's guide. Cambridge, England: Cambridge University Press.
- McCabe, V., & Balzano, G. L. (Eds.). (1986). Event cognition: An ecological perspective. Hillsdale, NJ: Erlbaum.
- McCarthy, D., & Davison, M. (1979). Signal probability, reinforcement, and signal detection. *Journal of the Experimental Analysis of Behavior*, 32, 373-386.
- Michon, J. A., & Jackson, J. L. (Eds.). (1985). Time, mind, and behavior. Berlin: Springer-Verlag.
- Newhall, B. (1982). The history of photography: From 1839 to the present (rev. ed.). New York: Museum of Modern Art.
- Richelle, M., & Lejeune, H. (1980). Time in animal behaviour. London: Pergamon.
- Roitblat, H. L. (1987). Introduction to comparative cognition. New York: W. H. Freeman.
- Schiffman, H. R. (1990). Sensation and perception (3rd ed.). New York: Wiley.
- Shimp, C. P. (1976). Short-term memory in the pigeon: Relative recency. Journal of the Experimental Analysis of Behavior, 25, 55-61.
- Speich, M. L., & Rusak, B. (1992). Time present and time past. In W. K. Honig & J. G. Fetterman (Eds.), *Cognitive aspects of stimulus control* (pp. 47-67). Hillsdale, N.J. Erlbaum.
- Staddon, J. E. R. (1983). Adaptive behavior and learning. New York: Cambridge University Press.
- Staddon, J. E. R. (1984). Time and memory. In J. Gibbon & L. Allan (Eds.), Annals of the New York Academy of Sciences: Vol. 423. Timing and time percep-

tion (pp. 322-334). New York: New York Academy of Sciences.

- Stephens, D. W., & Krebs, J. R. (1986). Foraging theory. Princeton, NJ: Princeton University Press.
- Stubbs, D. A. (1976). Response bias and the discrimination of stimulus duration. Journal of the Experimental Analysis of Behavior, 25, 243-250.
 Stubbs, D. A. (1979). Temporal discrimination and psy-
- Stubbs, D. A. (1979). Temporal discrimination and psychophysics. In M. D. Zeiler & P. Harzem (Eds.), Advances in the analysis of behavior: Vol. 1. Reinforcement and the organization of behavior (pp. 341-369). Chichester, England: Wiley.
- Stubbs, D. A. (1980). Temporal discrimination and a free-operant psychophysical procedure. Journal of the Experimental Analysis of Behavior, 33, 167–185.
- Stubbs, D. A., Dreyfus, L. R., & Fetterman, J. G. (1984). The perception of temporal events. In J. Gibbon & L. Allan (Eds.), Annals of the New York Academy of Sciences: Vol. 423. Timing and time perception (pp. 30-42). New York: New York Academy of Sciences.
- Szarkowski, J. (1989). Photography until now. New York: Museum of Modern Art.
- Wilkie, D. M. (1987). Stimulus intensity affects pigeons' timing behavior: Implications for an internal clock model. Animal Learning & Behavior, 15, 35-39.
- Woodrow, H. (1951). Time perception. In S. S. Stevens (Ed.), Handbook of experimental psychology (pp. 1224– 1236). New York: Wiley.
- Zeiler, M. D. (1991). Ecological influences on timing. Journal of Experimental Psychology: Animal Behavior Processes, 17, 13-25.

Received April 26, 1993 Final acceptance January 25, 1994