TEMPORAL REPRODUCTION

MICHAEL D. ZEILER AND MARK S. HOYERT

EMORY UNIVERSITY AND INDIANA UNIVERSITY NORTHWEST

A signal appeared for a certain time period. After the period elapsed, pigeons had to begin and complete a sequence of 15 responses in a time window ranging from the signal duration to 50% longer. Sessions involved as many as 10 different signal durations occurring in a random sequence. The times produced by pigeons often were in the same ranges as those that have been found with adult human subjects. The average times were described equally well as linear or power functions of signal duration. However, instead of the overestimation of durations usually found when animals have timed the duration of antecedent stimuli, the linear functions suggested that the pigeons underestimated the durations of their own behavior. The birds showing the strongest control when the conditions involved eight or 10 different duration requirements revealed the constant coefficients of variation that support Weber's law and scalar timing theory. Scalar timing in temporal differentiation appears to depend on non-ambiguous information about the duration required for reinforcement and on a high degree of sensitivity to the duration requirement.

Key words: timing, reproduction, temporal differentiation, scaling, sensitivity, key peck, pigeons

The nature of timing seems to depend on whether animals must time the duration of an antecedent stimulus or must time their ongoing behavior. When animals have had to evaluate the duration of stimuli (temporal discrimination), their accuracy was always the same when calculated relative to the length of the stimulus. Such behavior reflects the constant proportionality between the range of errors and time estimation that is predicted by both Weber's law and scalar expectancy theory (Church & Gibbon, 1982; Gibbon, 1977). If, however, they had to coordinate their behavior with temporal demands operating with respect to its onset time, duration, or cessation (temporal differentiation), Weber's law and scalar theory have not held (Cantor & Wilson, 1981; Platt, 1979; Zeiler, 1983). How they estimated the duration of critical durations also has differed. In discrimination, animals usually overestimate the duration of the stimulus by a constant proportion (Church, Getty, & Lerner, 1976; Church & Gibbon, 1982), but, in differentiation, animals typically exceed or match short requirements and fall short of longer ones. The timing of responses has shown a power relation to the minimum time requirement (Catania, 1970; DeCasper & Zeiler, 1977; LeJeune &

Jasselette, 1986; Platt, 1979) rather than the linear relation appearing in the timing of stimuli. Only when the differentiation procedure has been altered to preclude the need to respond when the reference time has elapsed has the timing of responses appeared similar to the timing of antecedent stimuli (Zeiler, 1985).

Does this necessarily imply fundamental differences in the nature of timing depending on whether it involves external stimuli or ongoing behavior? Perhaps. Before drawing such conclusions, it is necessary to recognize that experiments on discrimination have involved a precisely defined standard duration but those on differentiation have not. What is the functional standard duration in temporal differentiation? Some aspect of experienced reinforced duration seems to serve as the reference point, because the animal never is exposed directly to the time requirement itself (Gibbon, 1977; Platt, 1979; Zeiler, 1983). A dynamic relation between ongoing behavior and reinforcement fits much that is known about operant behavior in general, and it probably characterizes the timing of responses as well. The first explicit attempt to develop a coherent explanation of differentiation appeared with Gibbon's (1977) hypothesis that mean reinforced duration provided the standard. However, when Kuch (1974) imposed both lower and upper bounds for reinforcement, response duration decreased along with mean reinforced duration, but the relation between them was not constant. Furthermore, because shortest

This research was supported by Research Grant BNS-8315480 from the National Science Foundation. Correspondence and requests for reprints should be addressed to Michael D. Zeiler, Department of Psychology, Emory University, Atlanta, Georgia 30322.

reinforced duration was unchanged, it did not explain the behavior either.

The need is for a differentiation procedure that employs a known standard. The method of temporal reproduction does exactly that. In reproduction—which is a common way of studying timing by humans (Eisler, 1976)—the subject is given a duration and then must produce one that matches it. Reproduction is a type of differentiation procedure in that the subject produces durations, but the procedure provides the standard duration explicitly.

Two experiments have used temporal reproduction with nonhuman subjects. Mandell and Atak (1982) found that (a) rats responded differentially to two signal durations; (b) they responded appropriately to novel signal durations between the two originals (1 s and 3 s), but not to those beyond this range; (c) the durations produced exceeded the 1-s requirement and fell short of the 3-s standard. This general function is typical of behavior found in other forms of temporal differentiation, but normally a 3-s requirement on bar-press duration would be overshoot rather than qualify as a long criterion (cf. Platt, 1979); (d) the data supported Weber's law, in contrast with what had appeared in other types of temporal differentiation; however, this conformity required invoking the operation of nonsensory processes; (e) the distribution of response durations was bimodal, which has always been found whenever temporal differentiation has involved the duration of bar presses. The other experiment (Eisler, 1984) used 10 different duration signals in each condition, but only 2 of 8 rats reproduced durations at all. Even for those 2, control by signal duration was weak. The existing data simply do not provide much quantitative information about temporal reproduction.

Humans may be instructed as to their tasks and can then perform without feedback, but nonhumans are shaped and maintained by the consequences of their behavior. If nonhumans are to be given food for correct reproductions, they cannot be required to match the signal duration exactly; therefore, a window is essential. Eisler's windows, however, extended either for less than half the duration of the standard to over twice as long as the standard or from the standard plus and minus 50%, which meant that the signal corresponded to neither the lower nor the upper bounds. Per-

haps the weak stimulus control reflected the lack of "demandingness" of the situation (Mandell & Atak's, 1982, window was far more stringent in being the duration of the signal plus or minus 25%, and they obtained much stronger control). In short, the existing data on temporal reproduction by nonhumans are ambiguous.

The present experiment added further information by studying temporal reproduction with pigeons. The response duration was the time taken to begin and complete a sequence of 15 responses. This sequence duration has generated the same conclusions about temporal differentiation as has every other temporal feature of behavior studied to date (DeCasper & Zeiler, 1977), and it has had the additional advantage of yielding unimodal distributions of response durations.

METHOD

Subjects

Four experimentally naive, adult female White Carneau pigeons (*Columba livia*) were maintained at about 80% of the free-feeding weights that were determined during their first 2 months in the laboratory. They were maintained at these weights by supplementary feeding immediately after each session, if necessary. The time of feeding on days when sessions were not conducted was variable. The birds had continuous access to water both in their living cages and in the experimental chamber.

Apparatus

The experimental chamber was 36 cm long, 32 cm wide, and 35 cm high. The walls and floor were lined with unpainted aluminum, and the pigeon stood on a platform constructed of wood dowels each separated by 2.6 cm and raised 5 cm above the floor. Two 1-W white lights, each located in an upper corner of the response panel, provided general illumination. The panel also contained three 1.9 cm diameter horizontally aligned keys (Gerbrands), each 21 cm above the floor and 8 cm apart. The left key was dark and inoperative. The center and right keys could be illuminated from behind by two 1-W red and blue lights, respectively. The keys were activated by a force of at least 0.18 N. A 5-cm square aperture beneath the center key and 9 cm from the floor allowed occasional access to Purina® Pigeon

Checkers, the birds' standard diet. During the 4-s feeder cycles, the aperture was illuminated by a 1-W white light, and the keylights and houselights were turned off. Continuous white noise helped mask extraneous sounds. Experimental events were programmed and recorded by a Digital Equipment Corporation PDP-8A® computer operating under SUPERSKED® software (Snapper & Inglis, 1979).

Procedure

Sessions were conducted 5 or 6 days per week, except for holidays and short vacation periods. Each session ended either after 30 food deliveries or 90 min, whichever occurred first.

After the pigeons were trained to eat from the food hopper, they were shaped to respond to the key by providing food for successively closer approximations to a key peck. They then were trained to emit 15 responses to the lit center key per food delivery (fixed-ratio schedule). This procedure was maintained for 21 sessions of 30 food deliveries each.

The next phase involved single time requirements. Each cycle began with the center key darkened and the right key (signal key) illuminated for 8 s. This was followed by 0.5 s with both keys dark, and then by the illuminated center key. The 15th response to the center key turned the light off. Food was delivered if the period of center-key illumination (the ratio time) exceeded 8 s. If the ratio time did not exceed 8 s, the chamber was darkened for 25 s. The cycle was then repeated. The 8-s signal duration continued for 12 sessions. Subsequent signals for the prevailing duration requirement were 15 s (30 sessions), 20 s (16 sessions), and 25 s (20 sessions).

The next sessions had two different signal durations occurring in a random sequence. The duration of signal-key illumination corresponded to the lower limit of the prevailing time requirement. From now on there also was an upper limit 1.5 times the value of the lower. If the ratio time was between the limits, the bird received food. If not, the chamber was darkened for 25 s. Incorrect ratio times were followed by reimposition of the same requirement (a correction procedure). Each pair of duration signals was imposed for 15 sessions. The lower bounds of the pairs were (in seconds): 6 and 12, 7 and 14, 8 and 16, 9 and 18,

and 10 and 20. The number of signals then was increased to three with each of the following trios used for 20 sessions each: 5, 10, and 20; 5, 10, and 15; 6, 12, and 18; 7, 14, and 21; 8, 12, and 16; 9, 14, and 19; and 10, 15, and 20. Next, there were four duration signals (5, 10, 15, 20) for 30 sessions and six (5, 8, 11, 14, 17, 20) for 40 sessions. The first condition of 10 duration signals (5, 7, 9, 11, 13, 15, 17, 19, 21, 23) followed for 20 sessions, and was succeeded by a condition involving eight signals (4, 5.2, 6.8, 8.8, 11.4, 14.9, 19.3, 25.1) for 20 sessions. The last two sets had 10 signals each, with each condition in effect for 20 sessions. The members of the second 10-member condition increased by a constant proportion of 20%: 5, 6, 7.2, 8.6, 10.4, 12.4, 14.9, 17.9, 21.5, 25.8; the members of the third increased by a constant proportion of 25%: 4, 5, 6.3, 7.8, 9.8, 12.2, 15.3, 19.1, 23.8, 29.8.

RESULTS

For reproduction to be a useful technique, it was essential that behavior be controlled by the signals. One possible source of confounding was transfer between successive trials. The pigeons might be controlled by what they had done just previously rather than by the signal. Because of the correction procedure, a sequence of trials with the same signal continued until a correct response occurred. This meant that the pigeon could ignore the signal on the correction trials and also that the behavior on these trials could encompass some sort of shaping process that might not relate to signal duration. The cleanest measure of control by signal duration, therefore, was the first ratio time of each sequence (the only noncorrection trial of the sequence). Another ambiguity occurred if the signal on a noncorrection trial happened to be the same as the one that had just been followed by food, because the behavior could have reflected transfer from the preceding trial rather than stimulus control. The best measure of stimulus control, therefore, was the behavior occurring after the signal changed from one duration to another. The "first ratio times" take these considerations into effect. They exclude all correction trials as well as the first ratio time occurring after a food delivery, if the signal duration happened not to change.

In actuality, the first ratio times were not very different from those generated by consid-

eration of all ratio times, except that the overall data sometimes were more orderly because they were based on more observations. Given that a sequence of trials involving the same signal duration had to end with a correct ratio time, the overall mean ratio time might seem forced to correspond more closely to the time requirement than would the mean of first ratio times. However, these potential biasing effects were small, because there were many incorrect ratio times in every condition.

The data presented are the means and coefficients of variation (CV) of the first and all ratio times over the last seven sessions of each condition. The tables also show the number of ratio times (N) entering into each measure. Each signal duration began a sequence of trials approximately equally often in each session, but the number of first times varied because of differences in how often the same signal reoccurred following a correct response. The total number of ratio times with each signal duration depended on how often a trial sequence involved that duration and how many successive trials occurred prior to meeting the duration requirement. Given that the number of trial sequences was about the same for each signal duration, the consistent increase in the number of total ratio times meant that more trials were needed on average to generate a correct response with progressively longer signals. Such effects have been commonly found in all prior studies of temporal differentiation (Zeiler, 1986); therefore, they are not unique to the reproduction procedure. These same relations characterized success with the first ratio times. There was no sign of a shaping effect over the course of the correction trials: It appeared that each ratio time from first to last was randomly selected from the overall distribution of ratio times.

One important issue was the stability of the coefficients of variation across the different signal durations, because this provided evidence for or against Weber's law and scalar timing. Previous research has evaluated stability or change simply through visual evaluation of curves, but such measures can be ambiguous

(Zeiler, 1986). The present assessments involved analyses of variance. The coefficients of variation were calculated separately for each signal for each of the final seven sessions. These seven values provided the variance necessary to determine the significance of the difference between the means over the seven sessions. It was necessary to base these tests on all of the ratio times, because there often were too few first ratio times per session to permit reasonable tests. However, the general correspondence between first and all ratio times in other respects suggests that the overall data were representative of the first times as well.

General Characteristics of Performance

Ratio time distributions. Figure 1 shows distributions of ratio times in the last seven sessions of the final condition (10 signals) for Bird 165. The shapes of these distributions were representative of those for all 4 birds in each condition, although they did not all peak at the same points nor necessarily have identical slopes. When frequency distributions were plotted in terms of 10ths of the lower bound, the mode of each moved progressively downward with longer signals. No outliers involving ratio times over 100 s occurred in the condition shown in the figure. When they did happen, they were excluded from all data analyses; they were equally likely to occur with all signals, and they clearly were unique, because virtually no ratio times were between twice the signal duration and 100 s.

Every condition yielded unimodal distributions of fixed-ratio durations under all signal durations for both first and all ratio times. Such unimodality has been true of all other experiments on temporal differentiation involving fixed-ratio sequences as well (see DeCasper & Zeiler, 1974).

Pause time and run time. Neither time to the first response nor time from the first to the 15th response showed any relation to the duration of the signal. As was found earlier (Zeiler, 1970), temporal requirements imposed on fixed-ratio sequences had their most orderly effects on the entire sequence. It ap-

Fig. 1. Probability distributions of first and all ratio times for each signal duration. Data are for the third condition with 10 signals for Bird 165.

Table 1
Ratio times: one signal.

Lower bound (s)	Bird 28			Bird 31			Bird 165			Bird 172		
	N	M	CV	N	M	CV	N	M	CV	N	M	CV
0	210	7.7	0.3	210	9.5	0.2	210	9.3	0.3	210	8.6	0.2
8	404	9.9	0.3	419	9.9	0.2	403	9.7	0.2	373	10.8	0.2
15	826	13.4	0.3	674	14.9	0.5	438	15.4	0.2	726	14.2	0.1
20	1,417	16.6	0.4	1,235	16.5	0.3	447	20.2	0.2	877	18.7	0.3
25	1,840	20.3	0.4	1,749	21.6	0.4	469	23.7	0.3	1,726	21.9	0.3

peared that tradeoffs occurred between initial pause time and the time spent responding, with the relevant duration being their combination.

Responding during the duration signal. The number of responses to the signal key during the duration signal was similar for 3 birds and considerably larger for the 4th. The average number of such responses in each of the last seven sessions of each condition was 10, 341, 8, and 12 for Birds 28, 31, 165, 172, respectively. No pattern of occurrence or relation to accuracy in reproduction or to signal duration appeared in any condition.

One Signal

The initial exposure to time criteria required no attention to signal duration, because only one requirement was in effect during a session. Table 1 shows that the mean of all ratio times increased with progressively longer signals (first ratio times were not considered, because only the first ratio time of each session met the criteria for inclusion), and average coefficients of variation usually increased along

with them. The pigeons revealed similar ranges of ratio times, extending from means of about 10 s with the 8-s signal to 20–24 s with the 25-s signal.

Power and linear functions were fit between signal duration and mean ratio time. As shown in Table 2, both types of function accounted for the results about equally well. (These functions were fit to all conditions. Exponents of all power functions always were less than +0.83, and coefficients always exceeded +1.5. Coefficients of all linear functions were less than +0.95, and intercepts always exceeded +1.9.) Coefficients of variation increased significantly ($p < .05$) over the four signals with Birds 28 and 31 but not with Birds 165 and 172 ($p > .10$).

Two, Three, Four, Six, and Eight Signals

The signal became relevant when sessions involved two or more different signal durations, because the same ratio times could not meet all criteria.

Two signals. Table 3 shows the data for

Table 2
Percentage of variance accounted for by linear and power functions.

Number of signals	Bird 28				Bird 31			
	First		All		First		All	
	Linear	Power	Linear	Power	Linear	Power	Linear	Power
1			99	97			97	96
2	93	93	98	98	93	93	95	96
3	95	96	98	98	83	81	95	96
4	89	78	99	99	84	76	94	95
6	92	92	99	99	73	69	94	95
8	87	82	98	98	62	55	97	99
10 (1)	77	79	97	98	23	26	91	94
10 (2)	71	74	80	81	64	71	88	93
10 (3)	88	92	95	97	56	58	78	86

conditions involving two signals. Although the means of first ratio times and the means of all ratio times increased with signal duration, the ranges of the effects were larger for Birds 165 and 172 than for Birds 28 and 31 (the 20-s signal generated means about twice as large with Birds 165 and 172 as it did for the other 2). Table 2 shows that for Birds 28 and 31 power and linear functions accounted equally well for the relation between signal duration and mean ratio time. The fits to first means were not equally good for Bird 165, and all fits were poor for Bird 172, mainly because 8-s and 9-s signals produced mean times larger than those generated by 12-s and 14-s signals. The coefficients of variation increased significantly ($p < .001$) with longer signals for all 4 birds.

Three signals. Table 4 shows that with three signals mean ratio times continued both to increase along with signal duration and to have larger ranges with Birds 165 and 172 than with Birds 28 and 31. Table 2 indicates that power and linear functions accounted for over 90% of the variance in the means of all ratio times. However, the first ratio times of Birds 31 and 172 were described less well. For these 2 pigeons a trend now began that was to continue for the rest of the experiment: Bird 31 had increasingly poorer fits between first ratio times and signal duration as the number of signals increased, and Bird 172 had improving fits. All 4 birds had significantly increasing coefficients of variation ($p < .001$) with longer signals.

Four, six, and eight signals. Table 5 shows that the 4 pigeons separated into two groups

as number of signals increased. Birds 165 and 172 revealed consistently better control by signal duration over both first ratio times and all ratio times as the number of signals increased, and they continued to produce the largest range of mean ratio times. Birds 28 and 31 still showed orderly effects, but their magnitudes lessened with more signals.

Bird 31 revealed decreasing control by signal duration as the number of signals increased. Even with four signals, where the degree of control was greatest, ratio times ranged from 6.0 to 10.1 s. With six signals, the means of the first ratio times covered a still smaller range. Eight signals yielded small differences between the means produced by the smallest and the largest.

Based on the joint criteria of orderliness and magnitude of effect, the degree of control by six and eight signals was greater for Birds 165 and 172 than for the others, and was larger for Bird 28 than for Bird 31. The poorest fits to first ratio times with Bird 165 occurred with four signals, which perhaps suggests that this may have been a transition point for shifting from one type of control to another. Fits to first ratio times were good with six and eight durations for that pigeon and with four, six, or eight signals for Bird 172. As seen in Table 2, only the overall means continued to be well described by linear and power functions for Bird 31.

The coefficients of variation changed significantly ($p < .01$) with four signal durations in all but Bird 172 ($p > .7$). With six and eight signals, Birds 28 and 31 had significantly changing coefficients ($p < .001$), whereas Birds

Table 2
(Continued)

Bird 165				Bird 172			
First		All		First		All	
Linear	Power	Linear	Power	Linear	Power	Linear	Power
		100	100			99	97
88	87	96	95	71	68	52	52
94	95	90	92	87	88	95	95
65	63	95	97	98	100	98	99
98	97	99	99	98	99	97	94
98	98	98	98	99	98	99	96
98	98	99	99	96	98	98	98
96	93	99	99	97	98	100	99
96	95	96	98	99	99	97	92

Table 3

First and all ratio times: two signals.

Lower bound (s)	Bird 28						Bird 31					
	First			All			First			All		
	N	M	CV	N	M	CV	N	M	CV	N	M	CV
6	71	5.3	0.1	448	5.6	0.2	72	5.4	0.2	371	5.6	0.3
12	70	8.2	0.3	845	8.5	0.3	72	7.8	0.2	735	8.3	0.4
7	61	5.7	0.1	486	6.3	0.2	61	5.5	0.3	440	6.2	0.3
14	61	9.1	0.3	956	9.6	0.4	61	8.3	0.2	808	9.1	0.4
8	72	6.8	0.1	631	6.9	0.2	58	6.3	0.3	544	6.8	0.3
16	72	10.2	0.3	1,237	10.6	0.4	57	8.6	0.5	1,322	9.9	0.4
9	65	7.5	0.2	697	7.7	0.2	68	8.0	0.3	444	8.1	0.3
18	65	10.8	0.3	1,477	11.2	0.3	68	9.6	0.4	1,414	11.2	0.4
10	62	8.4	0.2	730	8.6	0.3	69	8.5	0.4	669	8.5	0.4
20	62	11.5	0.2	1,955	12.7	0.4	69	10.9	0.6	1,336	12.1	0.5

165 and 172 showed no changes at all ($p > .6$). The shift from a changing coefficient with four signals to a stable one with six and eight is a further indication that four signals provided a transition point for Bird 165, where its performance then became like that of Bird 172. The stable coefficients for Birds 165 and 172 supported Weber’s law.

Ten Signals

Ten signals provided the most demanding conditions. Trends seen with six and eight signals continued under the 10-signal conditions regardless of variations in the similarity of signal durations.

Figure 2 shows that the mean of first ratio

Table 4

First and all ratio times: three signals.

Lower bound (s)	Bird 28						Bird 31					
	First			All			First			All		
	N	M	CV	N	M	CV	N	M	CV	N	M	CV
5	44	5.1	0.2	146	5.0	0.2	33	5.6	0.5	96	5.9	0.5
10	39	8.8	0.5	308	9.4	0.3	36	7.3	0.2	427	8.6	0.4
20	35	12.6	0.3	504	14.6	0.5	33	9.1	0.5	609	11.7	0.6
5	49	5.2	0.2	192	5.1	0.2	47	6.4	0.4	121	6.0	0.4
10	41	8.8	0.3	243	9.1	0.3	46	7.4	0.9	367	8.3	0.4
15	50	11.6	0.3	510	12.0	0.5	47	8.9	0.3	812	10.2	0.5
6	46	5.6	0.1	302	5.9	0.3	38	7.6	1.4	172	6.7	0.5
12	35	9.0	0.3	311	10.1	0.4	38	7.7	0.4	353	8.9	0.4
18	44	12.8	0.3	647	14.1	0.5	38	9.0	0.5	736	10.7	0.5
7	32	6.0	0.2	233	6.8	0.3	33	7.3	0.3	158	7.0	0.3
14	32	9.9	0.3	310	11.3	0.5	32	10.0	0.4	313	9.9	0.5
21	37	11.4	0.2	599	15.8	0.6	35	11.1	0.2	650	12.8	0.6
8	38	6.9	0.2	202	8.0	0.3	37	7.2	0.9	187	8.4	0.4
12	41	9.3	0.3	246	10.3	0.4	33	7.0	0.2	300	8.8	0.4
16	38	12.1	0.4	409	13.8	0.5	41	10.5	0.6	815	10.4	0.5
9	46	7.4	0.2	224	8.9	0.3	30	9.8	0.6	211	8.6	0.3
14	49	11.1	0.8	301	11.2	0.5	27	10.3	0.6	342	9.8	0.5
19	51	12.2	0.3	509	14.4	0.5	34	10.2	0.4	666	10.7	0.5
10	35	8.7	0.2	186	9.8	0.3	36	7.2	0.4	222	8.2	0.4
15	37	11.5	0.2	208	11.9	0.4	40	9.7	0.7	429	10.1	0.5
20	44	13.2	0.6	447	15.0	0.6	39	10.2	0.3	646	12.0	0.6

Table 3
(Continued)

Bird 165						Bird 172					
First			All			First			All		
<i>N</i>	<i>M</i>	CV	<i>N</i>	<i>M</i>	CV	<i>N</i>	<i>M</i>	CV	<i>N</i>	<i>M</i>	CV
58	7.4	0.2	198	7.9	0.2	65	9.5	0.2	188	8.5	0.3
58	12.4	0.3	214	12.1	0.3	65	11.6	0.2	464	11.1	0.3
63	8.3	0.2	164	8.6	0.2	59	10.5	0.2	209	10.0	0.3
62	13.7	0.4	359	13.8	0.3	58	13.9	0.2	645	12.7	0.3
57	9.5	0.3	237	9.0	0.3	51	12.8	0.3	370	13.6	0.3
58	17.0	0.3	438	14.8	0.3	51	16.9	0.3	668	15.3	0.4
69	10.9	0.3	187	10.4	0.3	53	14.7	0.2	288	13.8	0.3
69	16.8	0.4	367	17.2	0.3	52	17.1	0.3	660	14.7	0.4
66	15.5	0.3	190	11.5	0.3	57	16.9	0.2	295	16.8	0.3
65	23.9	0.3	303	21.3	0.3	57	23.4	0.3	543	21.0	0.4

times in conditions involving 10 signals varied with their durations. Mean first times for Bird 28 differed with signal duration, but, as in the case of the eight-signal set, they varied over a small range. Condition 2 produced the least orderly effects. Bird 31 showed marginal effects of signal duration. Birds 165 and 172, however, revealed orderly first ratio times over

all three conditions. Table 2 indicates that linear and power functions accounted for 93% to 99% of the variance in first ratio times for Birds 165 and 172, and as much as 92% of the variance in one condition for Bird 28. Bird 31 never yielded a good fit between mean first ratio time and signal duration.

As Table 6 shows, mean first ratio times

Table 4
(Continued)

Bird 165						Bird 172					
First			All			First			All		
<i>N</i>	<i>M</i>	CV	<i>N</i>	<i>M</i>	CV	<i>N</i>	<i>M</i>	CV	<i>N</i>	<i>M</i>	CV
47	6.5	0.3	96	6.3	0.3	36	11.1	0.5	262	8.8	0.3
51	12.5	0.2	319	12.6	0.5	30	12.7	0.3	385	11.6	0.3
45	22.4	0.3	255	18.5	0.4	28	16.1	0.4	538	15.1	0.5
57	6.8	0.4	133	7.8	0.6	50	9.4	0.3	177	9.2	0.2
45	12.4	0.5	171	13.5	0.5	40	11.7	0.2	234	10.9	0.3
47	16.8	0.3	154	16.2	0.3	48	14.0	0.3	459	13.9	0.4
49	10.0	0.5	240	9.1	0.5	40	9.4	0.7	80	8.7	0.3
42	16.6	0.4	133	15.7	0.4	50	12.6	0.1	233	12.8	0.3
52	19.7	0.3	210	18.0	0.4	50	16.0	0.5	532	14.9	0.4
43	10.6	0.3	128	9.2	0.5	43	8.2	0.4	228	8.2	0.4
45	16.2	0.3	129	16.1	0.3	43	13.5	0.2	273	13.1	0.3
46	20.4	0.3	281	19.0	0.3	46	16.9	0.5	532	16.0	0.6
42	10.3	0.3	127	9.3	0.4	46	8.8	0.2	201	9.6	0.3
45	15.4	0.4	159	15.7	0.4	46	12.9	0.4	277	12.7	0.3
43	18.1	0.3	183	17.0	0.4	46	15.2	0.2	429	14.6	0.4
51	10.1	0.3	176	9.8	0.4	47	9.9	0.5	195	10.4	0.3
42	14.5	0.3	116	16.0	0.3	51	15.0	0.3	332	13.2	0.3
44	17.4	0.3	209	17.9	0.3	42	15.8	0.2	584	14.9	0.5
43	12.7	0.3	178	12.8	0.5	40	10.8	0.3	179	10.8	0.3
50	17.3	0.3	171	16.6	0.4	35	15.8	0.4	274	14.2	0.4
48	18.5	0.3	351	17.6	0.4	39	17.8	0.3	434	15.7	0.5

Table 5
First and all ratio times: four, six, and eight signals.

Lower bound (s)	Bird 28						Bird 31					
	First			All			First			All		
	N	M	CV	N	M	CV	N	M	CV	N	M	CV
5	38	6.5	0.2	80	6.2	0.3	38	6.0	0.3	82	5.1	0.3
10	34	6.6	0.2	268	8.4	0.4	44	5.6	0.3	398	7.0	0.4
15	30	7.8	0.3	326	11.5	0.4	38	8.9	0.4	323	10.3	0.4
20	29	9.4	0.4	476	13.5	0.5	40	10.1	0.4	586	10.8	0.5
5	24	5.6	0.1	79	5.5	0.2	27	5.0	0.3	135	4.9	0.3
8	25	6.0	0.2	137	7.3	0.3	17	4.5	0.1	136	5.9	0.3
11	16	7.7	0.3	100	9.5	0.4	22	6.4	0.2	169	7.5	0.5
14	24	10.9	0.4	180	12.0	0.4	21	6.0	0.2	184	9.3	0.5
17	23	11.2	0.4	211	13.5	0.4	17	9.9	0.4	303	9.0	0.5
20	24	11.8	0.5	278	15.0	0.5	22	8.5	0.3	476	10.2	0.6
4	16	5.9	0.1	74	5.5	0.2	14	5.0	0.4	75	4.2	0.2
5.2	14	6.7	0.2	82	6.4	0.2	17	5.8	0.7	96	4.3	0.3
6.8	15	5.6	0.1	106	6.7	0.3	14	4.5	0.1	135	5.0	0.2
8.8	17	5.8	0.2	177	7.4	0.3	16	4.7	0.3	176	5.5	0.4
11.4	17	7.2	0.2	189	9.2	0.4	16	5.0	0.3	186	6.3	0.6
14.9	17	9.3	0.2	219	12.0	0.5	16	6.5	0.2	399	7.1	0.5
19.3	16	9.1	0.3	245	13.2	0.5	17	7.3	0.2	468	7.9	0.6
25.1	16	10.6	0.3	336	15.3	0.5	16	6.8	0.1	550	8.6	0.5

with 10 signals were based on so few observations that perhaps the observed orderliness in 3 birds was more remarkable than the lack of it in Bird 31. Figure 3 shows the relation between signal duration and the means of all ratio times. Fits for Birds 165 and 172 accounted for 92% to 100% of the variance (Table 2), and those for Bird 28 accounted for over 95% of the variance in two conditions. Fits for Bird 31 also improved considerably. The range of mean first and overall times continued to be considerably larger for Birds 165 and 172 than it was for Birds 28 and 31.

Figure 4 shows the coefficients of variation. Changes in the coefficients did not achieve statistical significance in any of the three conditions for Birds 165 and 172 ($p > .34$ in all). The coefficients did change significantly for the other 2 birds in all three conditions ($p < .01$). In short, the 2 pigeons most strongly controlled by the signals (Birds 165 and 172) showed constant sensitivity to duration signals, but the other 2 did not.

Eisler Exponents

Eisler (1976) reviewed the data on temporal reproduction by humans published between 1868 and 1975. He calculated the power func-

tion exponents (b) that described each experiment in the equation: $(T_v - T_o)^b = (T_T - T_o)^b/2$, where T_v is the duration produced by the subject and T_T is the sum of the signal duration and the subject's reproduction. The term T_o —Eisler's "subjective zero"—determines the coefficient of the power function relating the subjective experience of the reproduced time to the subjective experience of the signal duration plus the reproduced time. His review reports only exponents (b). Exponents ranged between 0.70 to 1.10 for adults and were about 0.60 for children. Later, his 2 rats that showed any control by signal duration at all yielded exponents of 0.55 and 0.45 (Eisler, 1984). Calculations for Mandell and Atak's (1982) experiment yield exponents between 0.49 and 0.69.

Table 7 shows the corresponding exponents for the present data calculated as described by Eisler (1976). Those for all ratio times with Birds 28 and 172 were at the bottom of the range found for adult humans, and Bird 165 was in the middle. Bird 31 had exponents like those of Eisler's best 2 rats. The exponents for first ratio times also were well into the human range with Bird 165 and at the edge with Bird 172.

Table 5
(Continued)

Bird 165						Bird 172					
First			All			First			All		
<i>N</i>	<i>M</i>	<i>CV</i>	<i>N</i>	<i>M</i>	<i>CV</i>	<i>N</i>	<i>M</i>	<i>CV</i>	<i>N</i>	<i>M</i>	<i>CV</i>
35	6.5	0.5	112	7.0	0.4	37	8.1	0.2	84	8.0	0.2
46	18.3	0.3	191	12.6	0.4	40	11.8	0.2	115	12.2	0.2
44	19.8	0.3	116	16.1	0.3	41	14.4	0.2	163	14.4	0.3
39	19.2	0.3	251	17.9	0.3	40	16.2	0.2	297	17.5	0.2
24	6.1	0.2	98	7.1	0.3	33	9.3	0.2	70	9.3	0.2
29	8.1	0.3	169	9.1	0.3	30	11.9	0.3	72	10.5	0.3
33	11.3	0.3	185	12.5	0.3	23	13.3	0.2	85	11.2	0.2
27	12.4	0.3	208	14.8	0.4	29	14.5	0.3	119	14.1	0.3
33	16.6	0.3	174	16.4	0.3	33	15.5	0.2	175	15.3	0.2
33	20.2	0.3	225	18.5	0.3	26	17.6	0.2	184	17.4	0.2
26	5.8	0.2	74	6.2	0.3	23	7.0	0.2	75	8.3	0.2
25	6.4	0.3	78	6.8	0.5	25	7.9	0.1	79	8.1	0.2
26	8.2	0.3	83	7.6	0.3	25	9.1	0.2	73	9.5	0.2
26	8.0	0.3	117	9.3	0.4	25	9.8	0.2	88	10.0	0.2
25	11.9	0.3	97	12.4	0.3	23	11.0	0.2	83	11.9	0.2
25	14.5	0.3	83	15.1	0.3	25	13.9	0.2	126	13.6	0.3
25	18.4	0.2	105	18.9	0.3	24	16.9	0.1	198	16.6	0.2
27	20.9	0.2	180	20.8	0.4	24	19.6	0.2	381	19.7	0.2

DISCUSSION

Ratio times depended on the duration of the signal used to indicate the prevailing requirement. Control by signal duration occurred with respect to both the first ratio time emitted when the signal changed and all ratio times occurring in a session. The temporal reproduction procedure proved effective in establishing control over the timing of a sequence of responses, and it produced results with pigeons similar to those obtained by other researchers with humans.

Previous data on the relation between required and emitted duration were better described by power than by linear functions, whereas those on temporal discrimination fit linear functions. The present results were fit almost equally well by either type of function, and there was no consistency in which type was even slightly better. However, even a linear function did not yield results corresponding to those of temporal discrimination procedures. There, animals consistently overestimated the stimulus duration by a fixed proportion, which meant that the linear function had a coefficient greater than 1.0. Now, however, coefficients of the best fitting linear functions always were between 0.11 and 0.95. Coef-

ficients less than 1.0 indicate that the mean ratio times produced by the animals always underestimated the duration of the signal. These results support prior conclusions that the timing in temporal differentiation is not the same as that in temporal discrimination. Timing one's own ongoing behavior is fundamentally different than timing the duration of antecedent stimuli.

The issue is more complex with respect to the accuracy of timing. All prior research on temporal differentiation has found that coefficients of variation increased with longer requirements, thereby implying that temporal differentiation followed neither Weber's law nor scalar expectancy theory. Now, however, the birds most strongly controlled by signal duration with eight or 10 signals (Birds 165 and 172) also had the stable coefficients of variation that support both Weber's law and scalar theory.

Weber's law was not supported when the procedure involved fewer than four signals. Nor did it ever describe the behavior of either of the 2 pigeons (Birds 28 and 31) showing the weakest control by signal duration. Therefore, the data showed a correlation between

Fig. 2. Mean duration of first ratio times for each condition involving 10 signals.

Fig. 3. Mean duration of all ratio times for each condition involving 10 signals.

number of signals, degree of stimulus control by the signal, and stability of the coefficient of variation.

The correlation makes some intuitive sense,

even if it follows from no current theory. With few signals, it is possible for an animal to treat each as an arbitrary discriminative stimulus and then to emit a response that is defined

Table 6
Ten signals: number of first trials and total trials with each signal.

Lower bound (s)	Bird 28		Bird 31		Bird 165		Bird 172	
	First	All	First	All	First	All	First	All
5	16	19	7	62	19	58	21	22
7	16	61	9	78	19	36	20	44
9	17	78	8	62	20	53	23	47
11	18	75	6	51	19	33	21	77
13	16	70	6	61	18	38	20	71
15	18	114	8	113	19	35	21	57
17	17	128	7	44	19	51	21	65
19	17	134	10	415	18	40	22	83
21	17	190	8	296	20	56	21	112
23	17	194	7	96	20	89	20	125
5	13	35	8	20	15	36	20	21
6	11	32	10	48	14	30	21	33
7.2	13	59	10	35	15	33	20	46
8.6	13	83	10	98	17	61	21	73
10.4	13	67	8	71	16	64	19	65
12.4	13	95	10	83	17	52	20	63
14.9	14	68	9	259	15	56	21	87
17.9	13	98	9	200	16	92	20	90
21.5	14	156	10	232	15	125	21	162
25.8	11	214	9	205	19	171	21	209
4	11	14	8	11	21	40	13	233
5	11	13	7	13	21	36	13	23
6.3	10	52	8	33	20	38	11	22
7.8	11	79	8	20	21	36	10	38
9.8	11	65	9	124	21	61	16	41
12.2	12	122	8	132	21	95	12	44
15.3	12	63	8	114	21	55	11	59
19.1	13	131	7	222	21	74	14	69
23.8	10	133	6	279	21	75	14	136
29.8	10	114	8	227	21	173	13	295

solely by its consequences. It would not matter if the antecedent stimuli differed in their duration or in their color. Under these circumstances, stimulus generalization is likely to occur, so the behavior with one stimulus is affected by that occurring with others and the duration requirement becomes ambiguous. The result is that the situation is somewhat like that involved in ordinary temporal dif-

ferentiation, so Weber's law continues not to hold. However, a large number of signals makes it more difficult to treat each separately and thereby enhances the significance of the continuum of shared variation. Animals may or may not make the transition from arbitrary stimulus control to matching their behavior to signal durations. It appears that Birds 28 and 31 never made the transition, or did so

Table 7
Power exponents (per Eisler, 1976).

Set size	Bird 28		Bird 31		Bird 165		Bird 172	
	All	First	All	First	All	First	All	First
1	0.72		0.75		0.88		0.76	
2	0.62	0.60	0.58	0.56	0.91	1.02	0.79	0.85
3	0.74	0.74	0.53	0.50	0.83	0.98	0.62	0.68
4	0.63	0.39	0.57	0.49	0.81	0.98	0.72	0.66
6	0.75	0.62	0.53	0.51	0.84	0.95	0.67	0.64
8	0.62	0.43	0.41	0.31	0.83	0.83	0.68	0.71
10	0.63	0.61	0.41	0.37	0.81	0.80	0.71	0.72

Fig. 4. Coefficients of variation for each condition involving 10 signals.

only partially, and Bird 165 did so completely only when the number of signals increased to six. Bird 172, in contrast, came under only weak stimulus control by arbitrary stimuli and shifted to matching with as few as four signals. When behavior does come under the control of signal duration, the relevant duration loses its ambiguity and Weber's law comes into play.

The basic argument is that successful reproduction with numerous duration signals reduces the ambiguity inherent in other differentiation procedures. Although other procedures depend on the consequences of behavior to define the target duration, reproduction uses an explicit signal to do so. As such, it seems to be the only differentiation procedure yet devised that substitutes unambiguous information for the need to abstract relevant procedural features from ongoing performance. The problem is that animals seem to differ in their ability to come under the control of the duration of signals spontaneously; the appropriate shaping procedures for accomplishing this goal have not yet been identified.

When the reproduction procedure is successful, it seems to involve a form of imitation in which the signal duration is the model and the animal emits a duration accordingly. In any event, the behavior occurring in this seemingly complex environment not only was orderly and lawful, but it revealed the scalar timing process absent from other "simpler" forms of temporal differentiation. If conformity to Weber's law is a valid criterion, it seems that it may be easier for animals to reproduce a range of different intervals than to produce even one duration repetitively.

REFERENCES

- Cantor, M. B., & Wilson, J. F. (1981). Temporal uncertainty as an associative metric: Operant simulations of Pavlovian conditioning. *Journal of Experimental Psychology: General*, *110*, 232-268.
- Catania, A. C. (1970). Reinforcement schedules and psychophysical judgments: A study of some temporal properties of behavior. In W. N. Schoenfeld (Ed.), *The theory of reinforcement schedules* (pp. 1-42). New York: Appleton-Century-Crofts.
- Church, R. M., Getty, D. J., & Lerner, N. D. (1976). Duration discrimination by rats. *Journal of Experimental Psychology: Animal Behavior Processes*, *2*, 303-312.
- Church, R. M., & Gibbon, J. (1982). Temporal generalization. *Journal of Experimental Psychology: Animal Behavior Processes*, *8*, 165-186.

- DeCasper, A. J., & Zeiler, M. D. (1974). Time limits for completing fixed ratios. III. Stimulus variables. *Journal of the Experimental Analysis of Behavior*, **22**, 285-300.
- DeCasper, A. J., & Zeiler, M. D. (1977). Time limits for completing fixed ratios. IV. Components of the ratio. *Journal of the Experimental Analysis of Behavior*, **27**, 235-244.
- Eisler, H. (1976). Experiments on subjective duration 1868-1975: A collection of power function exponents. *Psychological Bulletin*, **83**, 1154-1171.
- Eisler, H. (1984). Subjective duration in rats: The psychophysical function. *Annals of the New York Academy of Sciences*, **425**, 43-51.
- Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review*, **84**, 279-325.
- Kuch, D. O. (1974). Differentiation of press durations with upper and lower limits on reinforced values. *Journal of the Experimental Analysis of Behavior*, **22**, 275-283.
- LeJeune, H., & Jasselette, P. (1986). Accurate DRL performance in the pigeon: Comparison between perching and treadle pressing. *Animal Learning & Behavior*, **14**, 205-211.
- Mandell, C., & Atak, J. R. (1982). Temporal reproduction in the rat. *Behaviour Analysis Letters*, **2**, 141-151.
- Platt, J. R. (1979). Temporal differentiation and the psychophysics of time. In M. D. Zeiler & P. Harzem (Eds.), *Advances in analysis of behaviour: Vol. 1. Reinforcement and the organization of behaviour* (pp. 1-29). Chichester, England: Wiley.
- Snapper, A. G., & Inglis, G. B. (1979). *SUPERSKED*. Kalamazoo, MI: State Systems.
- Zeiler, M. D. (1970). Time limits for completing fixed ratios. *Journal of the Experimental Analysis of Behavior*, **14**, 275-286.
- Zeiler, M. D. (1983). Integration in response timing: The functional time requirement. *Animal Learning & Behavior*, **11**, 237-246.
- Zeiler, M. D. (1985). Pure timing in temporal differentiation. *Journal of the Experimental Analysis of Behavior*, **43**, 183-193.
- Zeiler, M. D. (1986). Behavior units and optimality. In T. Thompson & M. D. Zeiler (Eds.), *Analysis and integration of behavioral units* (pp. 81-116). Hillsdale, NJ: Erlbaum.

Received October 17, 1988
Final acceptance April 2, 1989