OPTIMAL TEMPORAL DIFFERENTIATION

MICHAEL D. ZEILER, GREGORY K. SCOTT, AND MARK S. HOYERT

EMORY UNIVERSITY

In order to illuminate a light signaling a correct response, adult humans had to space their button presses according to a range of time requirements. In some conditions, the spacing needed only to exceed a minimum duration; in others, it had to fall between lower and upper bounds. Mean inter-response times always exceeded the lower limit, and decreased the more stringent were the upper bounds. Variability of interresponse times increased with larger lower bounds, but was unaffected by the size of the upper bound. Feedback about the direction of errors in conditions involving both upper and lower bounds did not affect the means, but it did reduce variability. Predictions were derived from optimality theory, based on the assumption that the critical factor was minimization of the time between correct responses. Without upper bounds, the theory overestimated the mean interresponse times by about 10%; with upper bounds, the theoretical predictions corresponded closely to the actual data. The results did not appear to reflect a scalar timing process. Optimality theory, in contrast to Weber's law, correctly predicted the variety of curves relating sensitivity to duration requirements.

Key words: optimality, temporal differentiation, feedback, button press, adult humans

An evolutionary outlook on the temporal control of behavior may integrate observations previously viewed from perspectives of either psychophysics or reinforcement schedules. The psychophysical orientation has stressed such issues as the relation between physical and experienced duration, the validity of Weber's law, and the nature of the internal clock (e.g., Allan, 1979; Church, 1978; Gibbon, 1977). The schedule approach, in contrast, has considered how differential reinforcement correlated with temporal features of either the environment or of behavior determines response rate and the patterning of responses over time (e.g., Anger, 1956; Morse, 1966; Shimp, 1979). Regardless of rationale, interpretation, and species, however, all of this research necessarily entails the imposition of temporal demands on organisms, and all can be approached as problems in adaptation.

When viewed from the standpoint of optimal foraging theory (MacArthur & Pianka, 1966), solutions to temporal and other challenges represent maximally efficient behavior under particular sets of constraints. Optimal foraging (see Krebs & McCleery, 1984, for a review) explains behavior in terms of the role

it plays in natural selection. Despite its focus on ultimate or functional explanation, the theory transcends vague statements of evolutionary faith by assuming quantitative form based on hypotheses about the costs, benefits, and constraints operating in specific situations. To the extent that behavior does or does not conform to predictions, the hypotheses are or are not supported, even though the guiding principle of adaptation probably is inherently untestable.

In contrast with psychophysical, reinforcement schedule, and other psychological approaches, optimal foraging theory does not try to describe the events or processes currently controlling behavior. Even perfect predictability does not mean that the costs, benefits, and constraints entered into the optimality equation necessarily are being weighed in some direct way at the time that the behavior is occurring. They might be, but the immediate source of control could also be some other event or process that has evolved to yield the same outcome. As Shettleworth (1984) pointed out, different mechanisms can produce a given result, and she aptly summarized the discussion by quoting Lehrman (1970, p. 28): "Nature selects for outcomes, not processes of development."

Optimal foraging theory has been applied to timing in the context of experiments that had been viewed as studying bisection of du-

This research was supported by Research Grant BNS 83-15480 from the National Science Foundation. Reprints may be obtained from Michael D. Zeiler, Department of Psychology, Emory University, Atlanta, Georgia 30322.

rations by pigeons and rats. In one such study, either a short or a long fixed-interval (FI) schedule was in effect, but no signal indicated which one currently prevailed (Platt & Davis, 1983). Food was obtained from the short FI by responding on one key and from the long FI by responding on the other key. The pigeons began responding on the key correlated with the short FI, and, if they did not obtain food, then switched to the one correlated with the long FI. The measure of timing was when the switch occurred, because this presumably reflected how pigeons scaled duration. The switching point sometimes corresponded to the geometric mean of the two fixed intervals (as would follow from Fechner's law), but in other instances it did not. In contrast to the partial success of the geometric mean analysis, all of the data were described by an optimality equation based on the assumption that animals were behaving so as to obtain food most efficiently (Zeiler, 1986). The only information that this reanalysis provided about more immediate factors was the essentially negative suggestion that logarithmic scaling of duration was not the way that efficient food-getting was translated into the locally controlling event. If it was, the Fechnerian and optimality accounts should not have differed in their ability to describe the results.

The success of this first effort at relating timing to general adaptive principles led to the present examination of optimality as the explanation of a different manifestation of temporal control. One type of arrangement—the *temporal differentiation* procedure—demands that behavior meet some temporal specification. For example, in a differential-reinforcement-of-low-rate (DRL) schedule, only responses spaced appropriately in time result in food delivery. Temporal differentiation is particularly interesting, because it involves the coordination of action with time, a feature that would appear to have substantial generality in behavior occurring both outside of and within the laboratory.

The experiment was conducted with adult humans as subjects. A major reason for doing so was that information about temporal differentiation by humans was scanty. In reviewing techniques for studying human time estimation, Allan (1979) included none that only entailed consequences based on whether behavior did or did not meet a criterion. Nor has

research with humans on differentiation schedules entailed ranges of time requirements sufficient to provide systematic information about the nature of temporal control.

When, as in the experiments reported here, human subjects simply get feedback about "correctness" and "errors," the situation seems quite different from that obtaining when non-humans are obtaining food. The present hypothesis was that challenges of both sorts can be viewed as implicating similar processes, namely, that: (1) Subjects minimize the time between correct responses; (2) the effort entailed in making the response is so small as to be essentially irrelevant in determining the efficiency of behavior. Time minimization, then, became the only relevant factor in maximizing efficiency when outcomes depended upon particular spacing of responses. The total time is the sum of the time occupied by correct responses (T_C), that occupied by incorrect responses (T_I), plus that occupied by the consequences of correct (C_C) and of incorrect (C_I) responses, plus the time taken to initiate the interval (T_B). The average time between correct responses (T) is this total divided by the number of correct responses (N_C).

$$T = \frac{T_C + T_I + C_C + C_I + T_B}{N_C} \quad (1)$$

Equation 1 is not theoretical; it is an exact description of the average time to a correct response in an experimental arrangement involving subject initiation and conclusion of an interval that must meet some criterion if it is to be deemed correct. If the criterion of correctness entails only a lower bound, then C_I refers to durations that are too short; if correctness is defined in terms of both lower and upper bounds, then C_I is the sum of the time occupied by durations that are too short and the time occupied by durations that are too long.

Optimal behavior is that which yields the smallest possible value of T , and such minimization would occur if all responses were exactly at the lower limit of correctness. This could not happen, however, given the ubiquitous variability of emitted durations and the resultant probabilistic nature of behavior. Equation 2 takes these considerations into account by expressing all of the times as means rather than as totals: MT_C is the mean time

attributable to correct responses; MT_s and MT_L are the mean times spent in emitting too-short or too-long durations, respectively; MT_B is the mean time taken to press the start button; C_C , C_s , and C_L are the temporal consequences of a correct, a too-short, or a too-long duration, respectively; and P_C , P_s , and P_L are the probabilities of correct, too-short, and too-long durations, respectively.

$$T = \frac{P_C(MT_C + C_C) + P_s(MT_s + C_s) + P_L(MT_L + C_L) + MT_B}{P_C} \quad (2)$$

Equation 2, like Equation 1, states the procedural relation between mean response duration and its consequences. If either the means of the correct and incorrect durations or their probabilities were known in advance, the equation could be used to find the value of the other terms that would minimize T . This, of course, was not possible. What was possible was to conduct the experiment and compute the standard deviation of the actual response durations. Given the standard deviation, distributional statistics then could be used to determine the area under the curve (the probability of occurrence) and the mean value for any segment when the overall mean was set at some value. An iterative routine determined the smallest overall mean (T) that satisfied Equation 2, and this value was the one that optimized time between correct responses.

METHOD

Subjects

Four adult males (the co-authors of this paper and one other) served as subjects. None had previously participated in a timing experiment. No theoretical predictions were discussed in advance of data collection, nor could any optimality predictions be derived prior to that time. The only explicit plan was to provide systematic information on temporal differentiation in behavior of humans under conditions similar to those that had been studied previously with nonhuman subjects. The subjects differed with respect to knowledge of conditions: GKS knew the specifics of every condition; MDZ was aware of the types of procedure to be studied over the course of the entire experiment but not of the particular condition or duration requirement imposed in

a given session; MSH did not participate in discussions of conditions until after all data were collected. The fourth subject was totally uninformed. Although he had initially agreed to participate for the entire experiment, he later refused to take part in more than a sampling of conditions (11 of the 40). Because the 3 subjects who served in all 40 sessions differed in their knowledge of conditions, and the fourth had no knowledge at all of the research, the results would seem to have some generality.

Apparatus

A vertical panel atop a desk held six pilot lights and two response buttons. The lights were arrayed horizontally. From right to left, the lights were labeled "Ready," "Time Elapsing," "Error," "Short," "Correct," "Long." All experimental events were programmed and data were recorded by a Digital Equipment Corporation PDP-8A® computer operating on-line with Supersked® software providing temporal resolution of 0.01 s.

Procedure

When the ready light was on, a press of the start (right) button turned that light off and turned on the time-elapsing light. A subsequent press of the stop (left) button turned off the time-elapsing light and defined the response duration. The procedure involved interresponse-time differentiation, with the critical feature being the time between presses of the two buttons.

Subjects were not verbally informed about particular time requirements. They were instructed to press the start button to begin an interval, to press the stop button to end the interval, to attend to the task, not to use any timepieces, and to avoid conscious counting. Throughout the entire experiment, a given session involved one procedure and one duration requirement, and lasted until the subject produced 25 correct durations. The first 10 interresponse times did not count toward this total. All 4 subjects later reported that they had not been aware of counting or performing other collateral behavior during any session.

1. No upper bound. In the first procedure, the seven duration requirements were 0.5, 1, 2, 4, 8, 16, and 32 s. An interresponse time that matched or exceeded the requirement re-

sulted in 2-s illumination of the "correct" light. One that fell short of the criterion resulted in 5-s illumination of the "error" light. The order of values was randomly determined for each subject prior to the first condition. Responses had no programmed consequences during either the correct- or error-light periods.

2. *Lower and upper bounds with and without directional feedback: 50% rule.* Now a correct duration was an interresponse time that fell between lower and upper limits. The lower bounds were 2, 4, 8, and 16 s. The upper bound was set at the 50th percentile of the distribution of durations that had been correct in the first procedure. For the 2-, 4-, 8-, and 16-s lower bounds, respectively, the upper bounds were 2.55, 5.3, 10, and 21 s for Subject GKS, 2.4, 5, 9.5, and 18.5 s for MDZ, and 2.4, 4.75, 10.5, and 19.5 s for MSH.

Responses within the specified limits continued to produce 2-s illumination of the "correct" light. Conditions either did or did not involve feedback as to the nature of errors. In the feedback conditions, interresponse times that failed to meet the criteria were identified as too short or too long by 5-s illumination of the appropriately labeled stimulus light. In the no-feedback conditions, incorrect interresponse times resulted only in 5-s illumination of the light labeled "error." The eight conditions (four temporal criteria times two feed-

back conditions) were conducted in a predetermined random order for each subject.

3. *No upper bounds.* This procedure replicated the first one, but with a different random order of the seven minimum-duration requirements for each subject.

4. *Varied upper bounds with and without directional feedback.* Three lower bounds (2, 4, and 8 s) were each combined with three different upper bounds. The difference between this and the second procedure is that now the upper bound did not depend on characteristics of previous behavior. Instead, the upper bound was either 1.05, 1.1, or 1.2 times the lower bound. As in the second condition, each combination of lower and upper bounds was investigated with and without directional feedback about the nature of errors. These 18 conditions (three lower bounds times three upper bounds times two feedback conditions) were conducted in a different predetermined random order for each subject.

RESULTS

Data recording began after the 10th response or after the first correct response, whichever occurred last. By this time, behavior appeared stable: Means and standard deviations of the last 10 interresponse times of a session did not differ from those of the first 10 recorded interresponse times. Tables 1 and

Table 1
Predicted and obtained results: No upper bounds.

Lower bound	GKS			MDZ			MSH		
	SD	T Pred	T Obt	SD	T Pred	T Obt	SD	T Pred	T Obt
0.5	0.08	0.7	0.6	0.09	0.7	0.5	0.07	0.7	0.6
	0.08	0.7	0.6	0.10	0.7	0.6	0.06	0.7	0.6
1	0.19	1.4	1.2	0.14	1.3	1.1	0.18	1.4	1.5
	0.18	1.4	1.2	0.14	1.3	1.0	0.17	1.4	1.3
2	0.34	2.7	2.3	0.28	2.6	2.2	0.34	2.7	2.3
	0.33	2.7	2.4	0.23	2.5	2.1	0.40	2.7	2.4
4	0.76	5.4	5.1	0.66	5.3	4.7	0.63	5.2	4.6
	0.69	5.3	4.9	0.67	5.3	4.4	0.57	5.1	4.6
8	1.62	10.6	9.8	1.01	9.9	8.9	1.69	10.7	9.7
	1.49	10.5	9.1	1.00	9.9	8.6	1.63	10.7	9.7
16	3.35	21.1	19.6	2.66	20.3	17.1	2.78	20.5	18.7
	3.21	20.9	18.1	2.70	20.3	19.3	3.10	20.8	19.0
32	6.05	41.3	38.7	5.07	40.3	34.8	6.83	41.6	36.9
	6.00	41.2	37.8	5.17	40.3	34.6	7.15	42.2	37.6

Note: The first line for each lower-bound requirement is for the first exposure (Experimental Condition 1); the second line is for the replication (Experimental Condition 3).

Table 2
Predicted and obtained results: Upper bounds.

Lower bound	Upper bound	Feed-back	GKS			MDZ			MSH		
			<i>SD</i>	<i>T</i> Pred	<i>T</i> Obt	<i>SD</i>	<i>T</i> Pred	<i>T</i> Obt	<i>SD</i>	<i>T</i> Pred	<i>T</i> Obt
2	*2.55	FB	0.28	2.3	2.2	0.29	2.2	2.2	0.15	2.2	2.2
	2.4	NFB	0.27	2.3	2.1	0.48	2.2	2.2	0.48	2.2	2.2
	2.4										
4	*5.3	FB	0.70	4.6	4.7	0.74	4.4	4.5	0.31	4.4	4.3
	5.0	NFB	0.71	4.6	4.8	0.80	4.4	4.4	0.94	4.2	4.3
	4.75										
8	*10.0	FB	1.27	8.8	8.9	0.91	8.6	8.7	0.46	9.0	9.1
	9.5	NFB	1.86	8.6	8.7	1.45	8.6	8.8	1.32	9.1	9.0
	10.5										
16	*21.0	FB	2.67	18.1	17.9	2.70	17.0	16.9	1.39	17.6	17.7
	18.5	NFB	3.56	17.9	18.4	2.97	16.6	16.5	4.72	16.5	16.7
	19.5										
2	2.1	FB	0.21	2.0	2.0	0.14	2.0	2.0	0.25	2.0	2.1
		NFB	0.30	2.0	2.0	0.47	2.0	2.0	0.26	2.0	2.1
4	4.2	FB	0.47	4.1	4.1	0.24	4.1	4.1	0.30	4.1	4.1
		NFB	0.60	4.1	4.1	0.93	4.0	4.1	0.47	4.1	4.1
8	8.4	FB	1.34	8.1	8.2	0.55	8.2	8.1	0.71	8.2	8.2
		NFB	1.74	7.9	8.1	1.83	7.8	8.0	1.06	8.2	8.2
2	2.2	FB	0.21	2.1	2.1	0.18	2.1	2.1	0.18	2.1	2.1
		NFB	0.36	2.1	2.2	0.58	2.1	2.1	0.21	2.1	2.1
4	4.4	FB	0.53	4.2	4.2	0.33	4.2	4.2	0.43	4.2	4.2
		NFB	0.67	4.2	4.2	0.90	4.1	4.3	0.44	4.2	4.1
8	8.8	FB	1.17	8.2	8.4	0.93	8.3	8.4	0.82	8.3	8.3
		NFB	1.60	8.2	8.2	1.62	8.2	8.3	1.00	8.3	8.4
2	2.4	FB	0.16	2.2	2.2	0.23	2.2	2.2	0.09	2.2	2.1
		NFB	0.30	2.2	2.3	0.46	2.2	2.2	0.18	2.2	2.2
4	4.8	FB	0.48	4.4	4.4	0.57	4.4	4.3	0.40	4.4	4.3
		NFB	0.42	4.4	4.3	0.79	4.3	4.5	0.36	4.4	4.4
8	9.6	FB	1.31	8.6	8.7	1.16	8.7	8.8	0.85	8.7	8.7
		NFB	1.29	8.7	8.6	1.20	8.7	8.9	1.04	8.7	8.9

* 50th percentile of the correct distribution of the preceding condition. In vertical order, first value is for GKS, second is for MDZ, third is for MSH.

2 show the data for all of the conditions; these data were used in all of the following analyses. No results are shown for the 11 sessions conducted with the fourth subject, because the conditions were insufficient to provide functions. The results always were within the range of those obtained in the same conditions with the other three participants. The tables include the optimal mean interresponse time as derived from Equation 2 (predicted *T*). The interresponse-time distributions approximated normality, so the normal distribution was used to calculate probabilities from the standard deviations.

Both the lower limit of the duration requirement and the stringency of the upper bounds influenced mean interresponse time (see Figure 1). Data were combined for the

feedback and no-feedback conditions, because the effect of upper bound was independent of whether or not errors were differentiated. The interresponse times generally increased as the window for correct responses became larger.

Figure 2 shows the relation between the optimal and obtained interresponse times for conditions not involving upper bounds. Because original exposure (Procedure 1) and replication (Procedure 3) produced similar results, they are not distinguished. In 41 of the 42 cases (seven time requirements times 3 subjects times two replications), the obtained duration was shorter than that specified by the optimality equation. On average, the IRT produced differed from optimality by -10.5% .

The fit was closer in the procedures involving upper bounds. In the total of 78 condi-

Fig. 1. Mean interresponse times plotted separately for each lower bound (minimum correct IRT). The horizontal axes are scaled in terms of the factor by which the upper bound (maximum correct IRT) exceeded the lower; the points represented by infinity are those where no upper bound prevailed. Data are combined across conditions involving the presence or absence of feedback regarding direction of errors.

tions, the obtained response durations deviated from the predictions by an average of 0.7%. Figure 3 shows the proportion of measures that deviated by a given percentage (thereby indicating the probabilities of those deviations), where negative and positive values signify undershooting and overshooting, respectively. The mode of this distribution was 0% (perfect correspondence), and 96% of the observations were within 3% of the optimality prediction.

The standard deviations were influenced by the lower bound of the duration requirement, but they were not affected systematically by the size of the upper bound. For each upper bound and feedback condition, higher lower

Fig. 2. Mean interresponse time as percentage of the value specified by the optimality equation in conditions without upper bounds. The dashed lines are the curves of perfect correspondence between obtained and predicted time.

bounds yielded larger standard deviations; in contrast, the standard deviations did not change consistently with a given lower bound over the different upper bounds. Variability also was affected by the presence or absence of directional feedback about errors. Under all combinations of lower and upper bounds, directional feedback reduced the standard deviations.

If Weber's law held, the standard deviation divided by the mean—the coefficient of variation—would be constant. In conditions not involving upper bounds, the unfilled circles of Figure 4 show that for GKS and MSH the coefficients generally increased over the range of time requirements, and for MDZ they tended to decrease and then increase. The only support for Weber's law was the lack of consistent direction of deviation from constancy across subjects. The obtained points did track the predicted (filled) points, which were generated by dividing the standard deviations by the means predicted from Equation 2. Although the pairs of curves in each set rarely

Fig. 3. Relative frequency of deviations from optimality by a given amount in conditions with upper bounds.

corresponded (they could not because of the differences between predicted and obtained means), they were approximately parallel.

Figure 5 shows that, under the conditions involving upper bounds, the coefficients of variation predicted from the optimal foraging model often corresponded with those obtained (as they must, given the close agreement between the means), and that the predicted and obtained curves almost always moved in the same direction. In some cases both curves rose, in other cases they fell, in others they remained fairly constant, and in still others they were erratic. Directional feedback about errors reduced the coefficients without disturbing the correspondence between predicted and obtained values; regardless of form and height, the curves corresponded. At the same time, the constant coefficients of variation demanded by Weber's law described only a minority of the curves. In short, as in other studies of human timing (Allan, 1979), Weber's law did not fit the results. It also may be of interest that every type of curve depicting the Weber fraction that has been reported in the literature (constant, rising, falling, erratic) appears somewhere in Figures 4 and 5. These data imply that the Weber fraction represents something more than a human's sensitivity to a stimulus or response dimension; it also is a function of the specific environmental demands.

Fig. 4. Predicted (filled circles) and obtained (unfilled circles) coefficients of variation in conditions without upper bounds. The predictions were obtained by dividing obtained standard deviation of response durations by the mean predicted from the optimality equation (see text).

DISCUSSION

The major findings were (1) the interresponse times were determined by the duration requirements; (2) interresponse times decreased as the upper limit defining a correct response was decreased; (3) interresponse-time variability was unaffected by the stringency of

Fig. 5. Coefficients of variation in conditions with upper bounds. The columns represent the different upper-bound requirements, where 1.05, 1.1, and 1.2 represent the factor by which the upper bound exceeded the lower, and 50% refers to the conditions in which the upper bound was determined from the distribution of correct durations occurring in the absence of upper bounds. Squares are conditions with no directional feedback for errors; circles are conditions with directional feedback. Filled points are predicted values; unfilled points are obtained values.

the upper limit; (4) mean interresponse duration was unaffected by feedback about direction of errors (too long or too short), but variability decreased; (5) the absence of upper bounds yielded interresponse durations shorter than those that were optimal; (6) upper bounds resulted in durations that corresponded closely with those predicted by an optimality analysis. Each of these results will be discussed in turn.

That humans exposed to a temporal-differentiation procedure showed an orderly relation between required and emitted durations conformed to the results reported for other species (DeCasper & Zeiler, 1977; Platt, 1979). However, where nonhumans have tended to produce durations that exceed the lower limit with short requirements, generate durations that approximately match with an intermediate range, and then undershoot with long requirements, the humans always overshoot to some extent. A model of temporal differentiation (Zeiler, 1981) proposed that subjects alternate between temporal control and

a tendency to respond as if no time requirement prevails; it follows that the resulting behavior is not the product of temporal factors alone. When pure timing was observed through use of a procedure that eliminated the untimed responses, pigeons always produced mean durations that exceeded the requirement (Zeiler, 1985). The similarity of the present results to those implies that humans had little tendency not to time in the present situation.

Several investigators have found that performance was affected when upper limits (limited holds) were added to minimum-duration requirements. Kelleher, Fry, and Cook (1959) reported that upper bounds brought interresponse times closer to the lower bound in rats; Kuch (1974) showed that rats' bar-press durations decreased as the size of the upper bound was reduced. The present experiment demonstrated these same effects with human subjects.

The present data did differ from earlier ones with respect to variability. Whereas Kuch (1974) found that more demanding upper bounds reduced variability, the present experiment did not. The reason for this difference may be that more stringent upper bounds reduce the tendency for rats not to time, whereas the present human subjects had little tendency not to time in the first place. The progressive elimination of a second form of behavior is likely to reduce the standard deviation of durations if the distributions of durations controlled by the two different sources do not overlap.

Directional feedback apparently has somewhat different effects on humans than on pigeons, the only other species that has been studied with comparable procedures. For pigeons, visual stimuli indicating whether interresponse times had been too short or too long to qualify for food delivery had no influence on either mean interresponse time or variability (Staddon, 1969). The present research also showed no effect on mean duration, but it differed in revealing substantial effects on variability. Whether insensitivity to directional feedback is an intrinsic aspect of stimulus control in pigeons or whether it could be developed given appropriate training remains unknown. With respect to humans, increased variability without directional feedback probably reflects the ambiguity of errors. Without

feedback, the consequences of errors signify only that the duration was incorrect, without signifying why; with directional feedback, the consequences provide discriminative stimuli that guide behavior more precisely by signifying whether the durations were too short or too long.

The optimality analysis was based on the assumption that behavior would minimize the average time between correct responses. When the criterion for correctness was only that the interresponse time exceed a specified value, the optimality equation correctly predicted that the absence of upper bounds would result in larger mean interresponse times than would conditions involving upper bounds, but it overestimated the emitted durations by about 10% on average. The deviations are not readily explained at this time. Perhaps factors other than or in addition to time minimization were being optimized, and these as yet unrecognized constraints were responsible for reducing interresponse times below the levels now expected.

The equation dealt accurately with conditions involving both upper and lower limits on correctness. From a psychophysical perspective, these data suggest that the temporal standard was the predicted optimal duration, and behavior was veridical with respect to it. However, the results offer no clue as to how the optimal duration is represented locally. What is evident is that the optimality equation closely described salient characteristics of human temporal differentiation and thereby provided an explanation of timing at the ultimate or functional level.

In cases like the present one where optimization involves the density of events, optimality theory might seem identical to a molar theory of reinforcer maximization (e.g., Rachlin, Battalio, Kagel, & Green, 1981). However, the theories provide different types of explanation. In its concern with evolutionary significance, optimality describes the function that a given type of behavior serves in terms of natural selection, and in this sense explains why the behavior occurs. In contrast to this functional-ultimate explanation, theories like those of Rachlin et al. describe controlling processes operating in a given situation at a given time. Reinforcer maximization is a mechanistic explanation of the behavior, but optimality can be viewed as explaining why

reinforcement exerts its effects. From the perspective of maximization-theory-as-mechanism, the present results would indicate that interresponse times were sensitive to differential consequences of molar reinforcer density. However, conformity to optimality predictions might follow just as well from control by momentary events (cf. Shimp, 1979) as from sensitivity to molar variables. Optimality theory is neutral in this regard, because it remains uncommitted as to how adaptive principles are translated into local mechanism. Another alternative is that reinforcer-density maximization really is not a mechanistic explanation at all, but instead is a functional concept derivable from the general adaptive principle of efficiency maximization.

An important remaining question is that of variability. The data support no version of Weber's law, and thereby imply that scalar processes do not describe human timing. Although sensory limitations must influence the nature of optimality (cf. Treisman, 1975), the results support no unifying general principle of temporal sensitivity. Neither is it clear how the particular contingencies might have favored variable responding, because time between correct responses could have been perfectly minimized had the behavior been invariant. However, optimality theory should not be confused with hypotheses about what should happen in some ideal world; it always refers to adaptation in the context of existing constraints and overall fitness. Variability in biological systems is pervasive despite its apparent nonadaptiveness in specific situations; it may be an intrinsic characteristic that has no particular significance other than revealing the essentially probabilistic or error-prone nature of behavior. But the need for variability in providing the raw material for natural selection implies that perhaps it is adaptive in some way. A number of experiments have indicated that alternative courses of action are sampled even when exclusive responding is locally optimal (see Timberlake, 1984). Sampling may have evolved because it is a way of making the most of ever-changing environments. The situation outside the laboratory differs in many ways from that studied now; one difference is that frequent repetition of identical demands occurs rarely. Variability could have evolved as an overall optimizing strategy even though it may have maladaptive

consequences under certain conditions. Understanding of behavior requires consideration not only of the constraints operating under a specific set of conditions but also of those relevant to overall fitness.

REFERENCES

- Allan, L. G. (1979). The perception of time. *Perception & Psychophysics*, **26**, 340-354.
- Anger, D. (1956). The dependence of interresponse times upon the relative reinforcement of different interresponse times. *Journal of Experimental Psychology*, **52**, 145-161.
- Church, R. M. (1978). The internal clock. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior* (pp. 227-310). Hillsdale, NJ: Erlbaum.
- 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.
- Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review*, **84**, 279-325.
- Kelleher, R. T., Fry, W., & Cook, L. (1959). Inter-response time distribution as a function of differential reinforcement of temporally spaced responses. *Journal of the Experimental Analysis of Behavior*, **2**, 91-106.
- Krebs, J. R., & McCleery, R. H. (1984). Optimization in behavioural ecology. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (2nd ed., pp. 91-121). Sunderland, MA: Sinauer.
- 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.
- Lehrman, D. S. (1970). Semantic and conceptual issues in the nature-nurture problem. In L. R. Aronson, E. Tobach, D. S. Lehrman, & J. S. Rosenblatt (Eds.), *Development and evolution of behavior* (pp. 17-52). San Francisco: Freeman.
- MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *American Naturalist*, **100**, 603-609.
- Morse, W. H. (1966). Intermittent reinforcement. In W. K. Honig (Ed.), *Operant behavior: Areas of research and application* (pp. 52-108). New York: Appleton-Century-Crofts.
- 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.
- Platt, J. R., & Davis, E. R. (1983). Bisection of temporal intervals by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, **9**, 160-170.
- Rachlin, H., Battalio, R., Kagel, J., & Green, L. (1981). Maximization theory in behavioral psychology. *Behavioral and Brain Sciences*, **4**, 371-417. (Includes commentary)
- Shettleworth, S. J. (1984). Learning and behavioural ecology. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (2nd ed., pp. 170-194). Sunderland, MA: Sinauer.
- Shimp, C. P. (1979). The local organization of behaviour: Method and theory. In M. D. Zeiler & P. Harzem (Eds.), *Advances in analysis of behaviour: Vol. 1. Reinforcement and the organization of behaviour* (pp. 261-298). Chichester, England: Wiley.
- Staddon, J. E. R. (1969). The effect of informative feedback on temporal tracking in the pigeon. *Journal of the Experimental Analysis of Behavior*, **12**, 27-38.
- Timberlake, W. (1984). Behavior regulation and learned performance: Some misapprehensions and disagreements. *Journal of the Experimental Analysis of Behavior*, **41**, 355-375.
- Treisman, M. (1975). Predation and the evolution of gregariousness. I. Models for concealment and evasion. *Animal Behaviour*, **23**, 779-800.
- Zeiler, M. D. (1981). Model of temporal differentiation. In C. M. Bradshaw, E. Szabadi, & C. F. Lowe (Eds.), *Quantification of steady-state operant behaviour* (pp. 205-214). Amsterdam: Elsevier/North Holland Biomedical Press.
- Zeiler, M. D. (1985). Pure timing in temporal differentiation. *Journal of the Experimental Analysis of Behavior*, **43**, 183-193.
- Zeiler, M. D. (1986). Behavioral units and optimality. In T. Thompson & M. D. Zeiler (Eds.), *Analysis and integration of behavioral units* (pp. 81-116). Hillsdale, NJ: Erlbaum.

Received June 6, 1986

Final acceptance December 13, 1986